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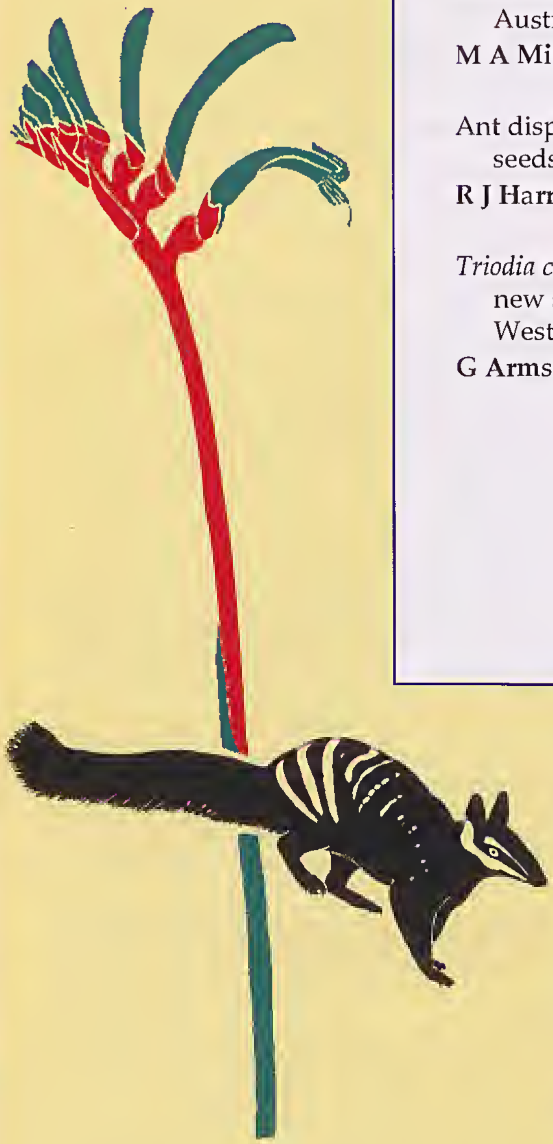

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Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor). The Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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Variation in age to first flowering and fruiting of *Banksia baxteri* and *Banksia coccinea* at the Stirling Range, south-western Australia

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Abstract

Age of first flowering (juvenile period) and fruiting were compared between cohorts of *Banksia baxteri* and *Banksia coccinea* established following fires in autumn 1989 and spring 1990 at a uniform site in the Stirling Range, south-western Australia. Following the 1989 fire both species commenced flowering by the time that plants were 59 months old, and more than 90% of individuals had flowered by the age of 97 months. By the age of 130 months 95% of plants of both species bore fertile cones. Both species took longer to reach reproductive maturity following the spring 1990 fire and only 35% of the *B. coccinea* cohort survived at the end of the 157 month study period. Very much below average rainfall in 1994 may have delayed flowering and cone production amongst the spring 1990 cohort which were still in the juvenile stage at the onset of the dry conditions. Intra-species variation in juvenile period has been documented for a range of plants in south-western Australia and warrants consideration in models of plant population dynamics.

Keywords: *Banksia*, mallee-heath, juvenile period, fire, south-western Australia

Introduction

Life history attributes provide important information about the ability of plants to persist under different fire regimes (Whelan *et al.* 2002; Burrows *et al.* 2008). Juvenile period, which is the period between plant establishment and first flowering, is commonly used as an indicator of the minimum inter-fire period required for persistence of fire sensitive plants that rely for regeneration on seeds held in serotinous fruits. Mature plants killed by fire release stored seeds, providing opportunity for recruitment of a cohort of seedlings. Seedling recruitment may be affected by a variety of factors in the post-fire environment including seedbed receptivity, seed predation, and climatic conditions. Replenishment of seed stores following fire may take considerably longer than the juvenile period. Minimum inter-fire periods of at least twice the juvenile period have been suggested for fire-sensitive shrub species in south-western Australian forests and heathlands (Gill & Nicholls 1989; Cowling *et al.* 1990; Witkowski *et al.* 1991; Burrows & Wardell-Johnson 2003; Burrows *et al.* 2008).

This paper reports observations of age of first flowering and fruiting for cohorts of *Banksia baxteri* (R. Br.) and *Banksia coccinea* (R. Br.) established following two fire events at adjacent sites in the Stirling Range, south-western Australia.

Study area

The study area was located near Two Mile Lake (34° 28.7'S, 118° 15.7'E) at an elevation of 180 m above sea level in the Stirling Range National Park, about 90 km north of Albany. This region of Western Australia experiences a moderate Mediterranean-type climate with cool moist winters and warm dry summers (Beard 1984). General features of the climate in the Stirling Range and surrounding areas are described by Courtney (1992). The nearest climate observation station is at Mettler (Bureau of Meteorology) which is located 25 km south-east of the study area and closer to the Southern Ocean. At Mettler the mean maximum temperature in the hottest month (January) is 25.1°C and mean minimum temperature in the coldest month (August) is 6.1°C. Annual rainfall at Mettler in the period 1966–2007 averaged 606 mm with a median of 611 mm. Until 1991 rainfall observations were also taken at Kojaneerup which is equi-distant between the study site and Mettler. Annual average rainfall at Kojaneerup (1961–1991) was 130 mm less than at Mettler. Descriptive rainfall categories and decile ranges referred to in this paper are as defined by the Bureau of Meteorology: very much below average (decile 1), below average (deciles 2–3), average (deciles 4–7), above average (deciles 8–9), very much above average (decile 10).

Soils at the study area are predominantly brown sandy-gravels with lateritic pisoliths (small ironstone nodules) interspersed in a mosaic of white sand sheets overlying laterite (Churchward *et al.* 1988). The dominant vegetation is *Eucalyptus tetragona* mallee-heath (Keighery and Beard 1993) with a diverse layer of low shrubs including Proteaceae (*Banksia, Hakea, Isopogon, Petrophile*), Myrtaceae (*Beaufortia, Calothamnus, Calytrix*) and Fabaceae (*Chorizema, Daviesia, Jacksonia*). Thickets of *B. baxteri* and *B. coccinea* occur on white sand substrates.

Methods

Flowering, fruiting and height growth were observed for cohorts of *B. baxteri* and *B. coccinea* regenerating following experimental fires conducted in March 1989 and November 1990 which consumed all leaf litter on the ground and the foliage on live shrubs. Prior to the experimental fires, the site had been unburnt since 1969. Areas burnt in 1989 and 1990 were separated by a track but were otherwise uniform in aspect, slope, surface soil characteristics and vegetation. In August 1994 20 plants of each species were selected at random within the areas burnt in 1989 and 1990. Individual plants were identified with a numbered tag, the number of flowers and fertile cones on each plant was recorded and the height of the growing tip was measured. Plants were re-measured in September 1995 and 1996, October 1997, May 1999, June 2000 and September 2004. The number of plants of each species that had flowered or produced fertile cones at each measurement date was expressed as a proportion of the number of individuals tagged at the commencement of the study without adjustment for mortality.

Results

Observations of post-fire regeneration made at the site indicate that seedlings of *B. baxteri* and *B. coccinea* emerge in late winter and early spring (August–September), regardless of whether the area was burnt in autumn or the previous spring. Nominal plant ages were assigned that assumed a delay between burning and seedling emergence of 6 months for the autumn cohort and 10 months for the spring cohort. Thus, at the commencement of the study the ages of seedling cohorts regenerated following the autumn 1989 and spring 1990 fires were respectively 59 and 35 months.

Autumn 1989 cohort

Most (90%) of the autumn 1989 cohort of *B. baxteri* tagged at the beginning of the study remained alive in September 2004 and attained an age of at least 181 months. Survival of B. *coccinea* was somewhat poorer and declined from 90% at 117 months to 75% at 181 months. The rate of height growth of *B. baxteri* was relatively consistent throughout the period of the study and surviving plants had an average height of 200 cm at an age of 181 months, while *B. coccinea* grew slightly faster and attained an average height of 245 cm at 181 months (Fig. 1). Both species had already begun to flower when the study commenced and 60% of *B. baxteri* and 65% of *B. coccinea* had at least one inflorescence by the age of 59 months (Fig. 2). By the age of 97 months 90% or more of plants of both species had flowered. Fertile cones with fully developed follicles were observed on 50% of *B. baxteri* plants by the age of 84 months, and 95% of plants bore fertile cones by the age of 97 months. Fertile cones were first observed on *B. coccinea* at the age of 84 months, but the proportion of plants bearing cones did not reach 95% until the age of 130 months.

Spring 1990 cohort

The spring 1990 cohort of *B. baxteri* exhibited good survival for the duration of the study with 90% of tagged individuals attaining an age of 157 months. Plants from the spring 1990 cohort exhibited a similar rate of height growth to the autumn 1989 cohort up until the age of 106 months but the rate of growth declined thereafter such that the average height was 119 cm by the end of the study (Fig. 1). Survival of the spring 1990 cohort of *B. coccinea* remained at 85% or greater up to the age of 86 months but had declined to 35% by the end of the study (157 months). Height growth of the spring 1990 cohort was slower than that of autumn 1989 cohort particularly up to the age of 73 months, and there was substantial variability in height of surviving plants at the end of the study as reflected by the large standard error (Fig. 1).

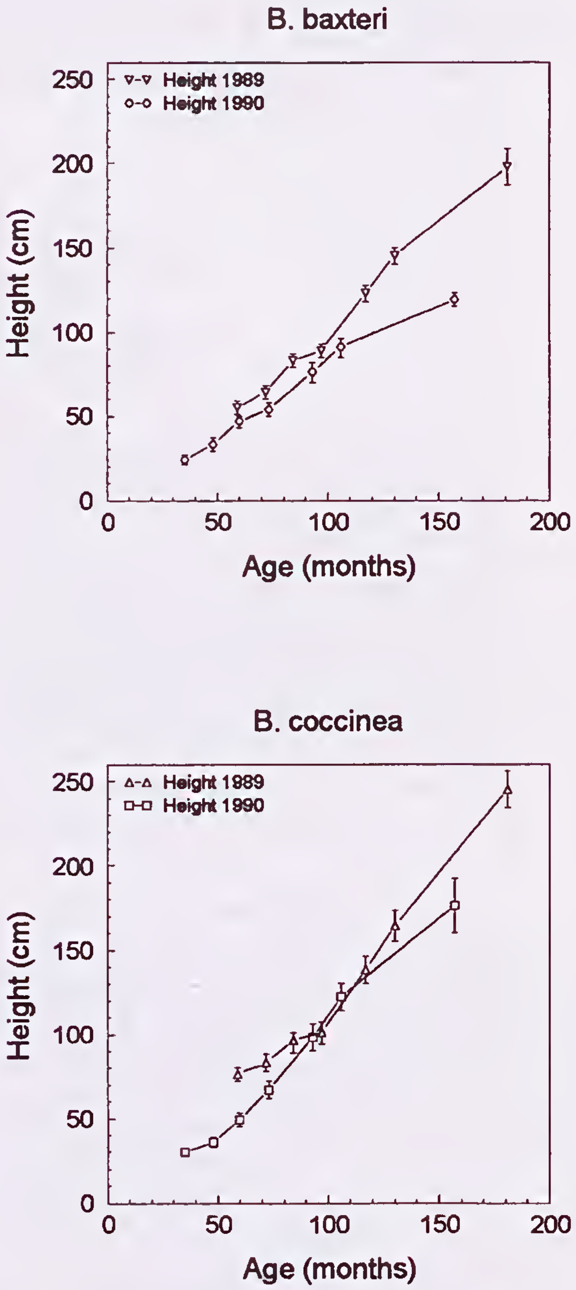

Figure 1. Height growth of *B. baxteri* (top) and *B. coccinea* (bottom) seedling cohorts regenerated following fires in autumn 1989 and spring 1990. Bars represent standard errors.

No plants of either species in the spring cohort had flowered by the age of 35 months when the study

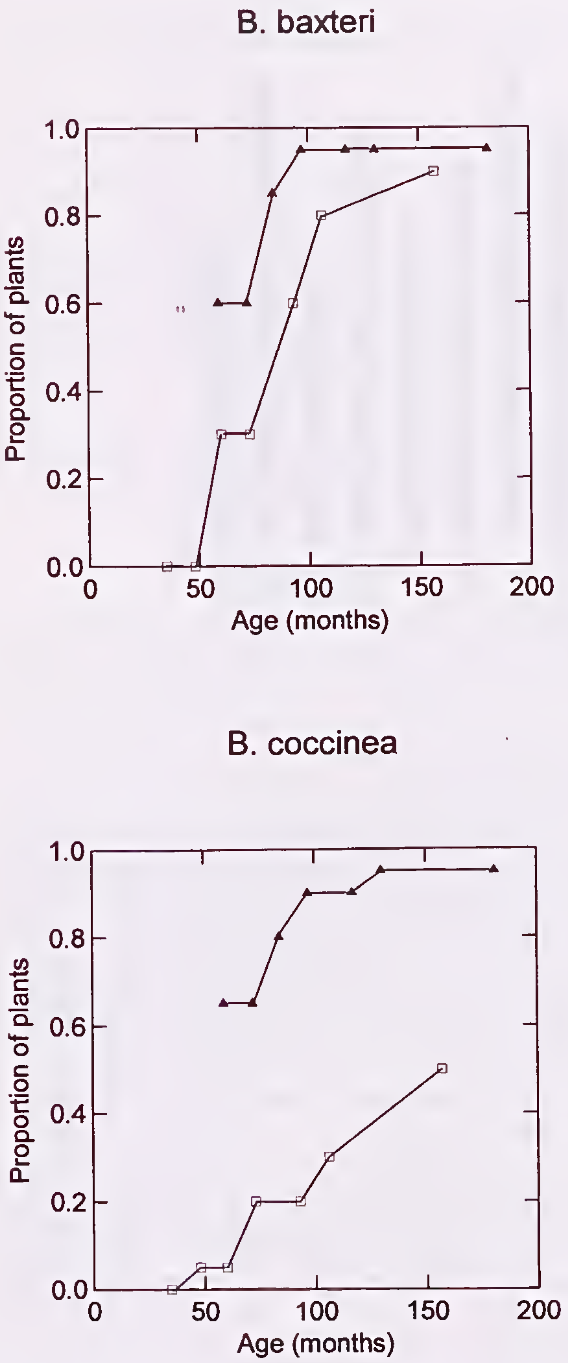

Figure 2. Proportion of plants of *B. baxteri* and *B. coccinea* flowering with increasing time since fire. Symbols represent cohorts regenerated following fires in autumn 1989 (triangles) and spring 1990 (squares).

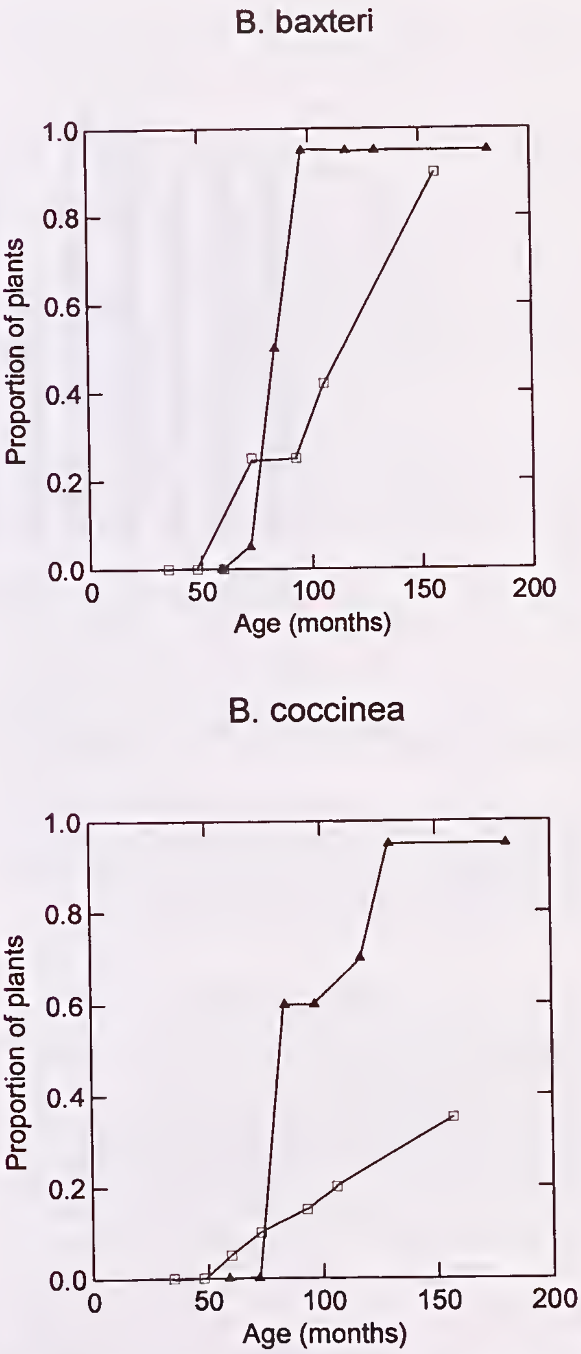

Figure 3. Proportion of plants of *B. baxteri* and *B. coccinea* bearing fertile cones with increasing time since fire. Symbols represent cohorts regenerated following fires in autumn 1989 (triangles) and spring 1990 (squares).

commenced. First flowers appeared on *B. baxteri* by the age of 54 months but it took 93 months for at least 50% of plants to flower and 157 months for >90% of plants to flower (Fig. 2). A small proportion of *B. baxteri* from the spring 1990 cohort developed fertile cones at first flowering but overall the spring cohort developed fertile cones at a slower rate than the autumn 1989 cohort (Fig. 3). Flowers first appeared on a small number of *B. coccinea* by the age of 48 months but only 50% of plants managed to flower during the 157 month period of the study (Fig. 2), some of which later died. Only (40%) of *B. coccinea* from the spring 1990 cohort developed fertile cones during the study and this took place more slowly than for the autumn 1989 cohort.

Rainfall during the period of the study

Rainfall at Mettler was average to above average from 1989 to 1993 during the period when seedlings emerged and commenced the juvenile growth phase (Fig. 4). Rainfall in 1994 was the lowest on record with only 379 mm recorded for the year and four consecutive months of very much below average rainfall between January

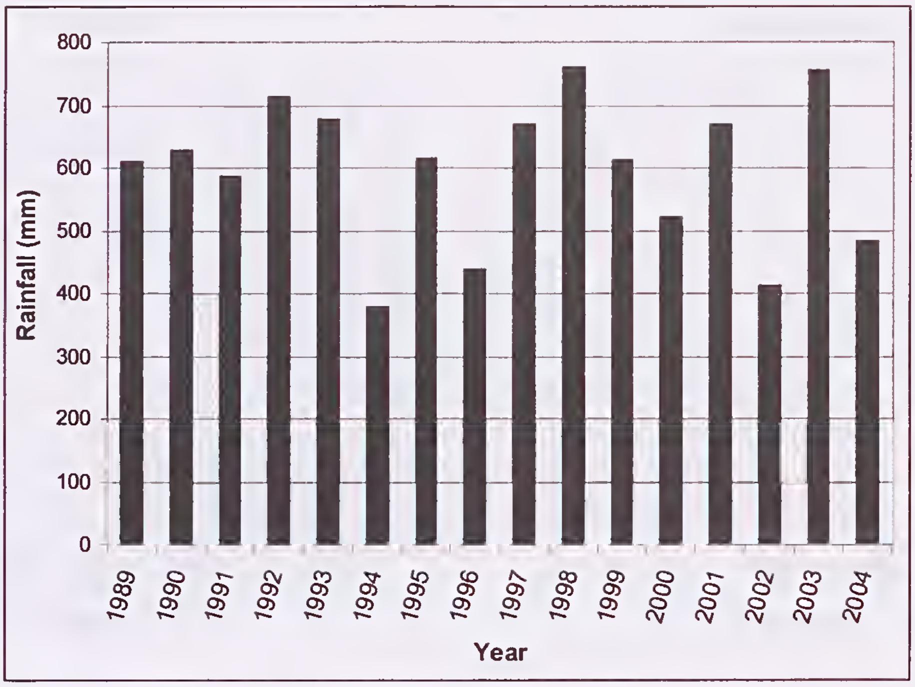

Figure 4. Annual rainfall at Mettler during the period 1989–2004.

and April. Further years of very much below average rainfall occurred in 1996, 2002 and 2004. Rainfall was very much above average in 1998 and 2003.

Discussion

Juvenile period length and timing of fertile cone production on *B. baxteri* and *B. coccinea* varied substantially between the two cohorts established following different fire events at the Stirling Range, even though both cohorts grew on an apparently uniform site. Wooller *et al.* (2002) reported that *B. baxteri* in the Fitzgerald River National Park flowered for the first time 60–72 months after fire which is similar to observations for the autumn 1989 cohort at the Stirling Range. They also observed that the proportion of plants flowering in any one year rose rapidly, peaking at close to 100 per cent after 180 months and gradually declining thereafter. Witkowski *et al.* (1991) reported that coastal populations of *B. baxteri* and *B. coccinea* at Hopetoun flowered for the first time 36 months after fire and produced fertile cones after 60 and 36 months respectively. The shorter juvenile periods at Hopetoun may reflect more favourable growing conditions due to coastal proximity compared with the sites examined by Wooller *et al.* (2002) and at the Stirling Range in this study. Post-fire juvenile periods of 639 plant species from the jarrah (*Eucalyptus marginata*) forest were examined by Burrows *et al.* (2008) who found that all species in their study flowered within 60 months of fire, and most flowered within 36 months. Burrows *et al.* (2008) noted that a number of widely distributed species had longer juvenile periods in drier eastern forest where annual rainfall is 750 mm or less.

Differences in environmental conditions during the post-fire juvenile period are a possible reason why the spring 1990 cohort took longer to flower and produce fertile cones. Seedlings established following the autumn 1989 fire experienced average to above average rainfall during four of the five years up to August 1994 when plants were first examined. In contrast, seedlings established following the spring 1990 fire experienced only two years of average or above average rainfall (1991–1993) before encountering very much below average rainfall in 1994. Dry conditions in 1994 and again in 1996 may have delayed flowering and cone production amongst this cohort.

Summer lightning storms are common in the Stirling Range and experience has shown that it is unlikely that fire can be excluded for more than a decade or two from the extensive tracts of mallee-heath that adjoin the range (McCaw & Gillen 1993). The rate of fuel accumulation in mallee-heath is such that fire can re-burn the same area after about 8 years (Keith *et al.* 2002). Data from this study indicate that provided growing conditions are favourable, *B. baxteri* and *B. coccinea* can produce fertile cones within 8 years (96 months) of establishment although maximum seed production is unlikely to occur until plants are about twice this age (Wooller *et al.* 2002). However, achievement of reproductive maturity may be delayed by adverse conditions in the post-fire environment. Land managers may choose to delay introducing planned fire to areas where seed stores are known to be limited, but must recognise that unplanned fires also pose a risk to plant communities in a post-fire recovery phase. For *B. baxteri* and *B. coccinea*, and similar taxa with on-plant seed storage, the risk of regeneration failure following fires at less than 10 years intervals will be reduced when some mature plants survive fire to provide a continuing supply of seed. Risk of localised extinction is greatest when all mature plants are killed by fire and the population is reduced to an even-aged cohort of juvenile plants that may be vulnerable to grazing or extremes of temperature (O'Brien 1989; Groom *et al.* 2004).

Models of plant population dynamics based on juvenile period and other life history attributes can provide important insights into the mechanisms by which populations persist in fire-prone environments (Enright *et al.* 1998). Some models have sought to incorporate the effects of seasonal weather conditions on seedling recruitment (Enright *et al.* 1998). Intra-species variation in juvenile period has been documented for a range of plants in south-western Australia and warrants consideration in models of plant population dynamics.

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Patinated glass from Cossack, Western Australia

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Abstract

The weathering of anthropogenic glass buried in a refuse site for 70–100 years in calcareous quartz sand at Cossack, Western Australia, in a tropical arid climate, has produced a patina (a thinly-laminated encrustation on the glass), some 6–100 µm thick. The patina was studied by Scanning Electron Microscopy (SEM), Energy Dispersive Spectroscopy (EDS), and X-Ray Diffractometry (XRD) to ascertain its structure and chemistry. In contrast to the structureless glass, SEM shows the patina to be comprised of micro-structures of planar to undulating lamination, micro-unconformities, and micro-cavities. The relationship of patina to parent glass shows it to be invasive (corrosive) into the glass, producing pitting along its contact, indicating dissolution, with the patina accreting at the expense of the (metastable) glass. The flatness of the upper surface of one sample of patina suggests little upward accretion. The locally-undulating upper surface of the other samples of patina, and the mosaic nature of the crust suggest there has been at least some outward (upwards) accretion. EDS shows the glass to be mainly Si, Ca, and Na, and the patina to be dominated by Si and generally depleted of Na. The patina is enriched in Ca, and this is interpreted to be exogenically derived from the surrounding calcareous quartz sand. There also appears to be enrichment of Fe, Al, and K in the patina, derived exogenically from the surrounding sand and dust. XRD shows calcite and aragonite in the patina. The patina on the glass from Cossack appears to involve solution and precipitation, vadose-zone illuviation, and accretion. There is solution of the parent glass, precipitation of silica as laminae in the patina, solution and precipitation of carbonate minerals, and solution of earlier-formed patina. In an environment where the pellicular water alternates between carbonate dissolving (and silica precipitating) and carbonate precipitating (and silica dissolving), carbonate minerals within the laminae of the patina, precipitated during the evaporation phase of any remaining pellicular water during the hot summer, is dissolved during the wet season to leave intra-patina cavities. Glass elsewhere in different environments globally show differences in style of weathering in terms of structures and lamination compared to the Cossack samples, indicating that it is probable that the environment of weathering influences the weathering micro-processes and hence result in different types of micro-structures and mineralogy in the weathering of glass and formation of patina.

Keywords: patina, glass, weathering, corrosion, Cossack, Western Australia.

Introduction

The weathering of glass is a phenomenon which has attracted the attention of industrial chemists, conservators, museum conservators, and archaeologists. It has been the subject of a number of studies into the effects that humid atmosphere (Newton 1976; Schreiner *et al.* 1999; Garcia-Valles *et al.* 2003; Fearn *et al.* 2004), seawater and sea-bed sediments (Weier 1973; Cox & Ford 1989; Brzezinski *et al.* 2003), soil (Brewster 1863; Brill 1961; Brill & Hood 1961), and groundwater (Cox & Ford 1993) have on glass.

The weathering of glass is dependent upon the composition of the glass itself, the nature of the surface of the glass, the surface area exposed (Frank 1982), and aspects of the environment (*e.g.*, the pH of the attacking solution, and temperature which act upon the glass: Newton 1971; Cox & Ford 1993). Weathering effects and products include: iridescence (Brewster 1863; Guillot 1934; Vader & Murray 1975; Pollard & Heron 1996); crusts (Newton 1971); leached layers (Schreiner *et al.* 1999); pits [surface pitting, this paper] (Maloney 1968; Garcia-Valles *et al.* 2003; Watkinson *et al.* 2005), plugs (Watkinson *et al.* 2005); crizells and dulling (Frank 1982; Fearn *et al.* 2004); and patinas (Garcia-Valles *et al.* 2003; this study). Weathered glass may be found in a variety of locations and environments: *in situ* (*e.g.*, medieval window glass in monasteries and cathedrals in Europe); in the marine environment (*e.g.*, glass artefacts from shipwrecks); in historic refuse sites in humid climates (*e.g.*, glass from the cullet heap at Bagot's Park, Staffordshire, England [Newton 1976]); and in historic refuse sites in arid climates (*e.g.*, flat glass and bottle glass from Cossack, Western Australia, this study).

The study of the weathering of glass is important for a number of reasons. Firstly, with the prolific use of glass in architecture in many polluted cities, its weathering is of concern as it affects the clarity and integrity of the glass. Secondly, glass has many applications in industry, one of the most important being the confining or storing of toxic waste products, including nuclear waste, in silicate glass matrices (Sterpenich & Libourel 2001), and how glass responds hydrochemically to fluids with which it is in contact is important in waste management. Thirdly, characterising glass decay that affects the stained-glass windows of centuries-old monasteries and cathedrals assists conservators whose aim it is to understand the processes of glass decay, and to restore and preserve such windows. Lastly, in the archaeological context, researchers have noted weathered surfaces on glass artefacts which, for instance, have been found in burial sites and in the remains of ancient cities, and have suggested its use for dating. In a field where absolute dating of glass artefacts at present is not possible, some researchers believe that weathering of glass could prove to be a dating method for some ancient glass (*e.g.*, the number of layers often found in any patina on glass being used in much the same way that tree rings are used to date wood [Brill 1961; Brill & Hood 1961]).

One of the products of weathering is patina, which is any fine layer or encrustation, usually laminated, on the surface of rock or other material (Bates & Jackson 1987). The term is also used with reference to the oxidation of metals such as bronze or copper, as well as for the layer on rock surfaces in arid regions (*e.g.*, "desert varnish", *cf.* Bates & Jackson 1987; Jackson 1997). While various terms have been applied to the products of weathering or corrosion products on the surface of glass (*e.g.*, "crust" [Newton 1971; Cox & Ford 1993]; "weathered crust", or "weathering crust" [Brill 1961; Brill & Hood 1961; Newton 1976; Cox & Ford 1993; Schreiner *et al.* 1996]; "corrosion crust" [Brill & Hood 1961; Cox & Ford 1989]; encrustations), the term patina was first applied to the weathering crust on glass by Garcia-Valles *et al.* (2003).

Definitions of the term "patina" vary, but there is a general consensus that it is any fine layer or encrustation on a given surface (Fowler & Fowler 1969; Wilkes & Krebs 1982).

Use of the term "weathering" or "weathered" for the altered surface of glass, for any crusts developed on glass, and for the development of the patina on glass at Cossack is only justified if the encrustations can be shown to be (at least in part) an alteration product of the parent glass and not merely a micro-sedimentary feature wholly accretionary on its surface (such as for desert varnish as suggested by Garvie *et al.* 2008; or similar to diagenetic or pedogenic accretionary features such as the laminae of calcrete ooids, other soil ooids, or ironstone pisolites; see Figure 7 in Read 1974, and Plates 73 and 81 in Brewer & Sleeman 1988). As will be shown later, that while there has been accretion of laminae in the "encrustations" on the glass from Cossack, there also has been corrosion and alteration of the parent glass, with remobilisation of Si and Na from the parent glass, which warrants the use of the terms "weathering" or "weathered". However, the "encrustations", as will be interpreted later, may be a complex product involving *in situ* alteration as well as accretion of laminae deriving from endogenic and exogenic sources. For this reason, for the glass from Cossack, the term "weathering" alone does not describe the processes that produce exogenic accretionary laminae, and the term "micro-sedimentation", if it were to be applied, also does not describe the processes that involve corrosion and the invasive alteration of the parent glass. Both processes are occurring, and therefore the term "patina" is used to refer to both the weathering products and micro-accretionary products developed on the glass from Cossack, Western Australia. Also, given the literature review above, use of the term "patina" in this study to refer to the laminated crust formed by weathering of glass at Cossack in Western Australia is appropriate, since it is both an encrustation and a product of weathering.

This study examines the patina on flat and bottle glass from Cossack, to ascertain the nature of the patina, and the potential source of the components of the patina (that is, whether it derives from the corrosion and reprecipitation of the primary material, and hence is endogenic, or has formed from an external source, *i.e.*, it is exogenic). To date, as noted earlier, much of the research into the weathering of glass has been undertaken in Europe and the United States of America and, in fact, much of the research in the last twenty to thirty years has focussed on the industrial applications of glass and the problems caused by corrosion of glass in that context. This study of the weathering of glass from Cossack is the first of its kind in Australia, and it contrasts with the weathering of glass described elsewhere (in submarine environments, buried in submarine sediments, buried in fresh groundwater environments, or exposed to humid atmosphere) because it is buried in a calcareous quartz sand located in a tropical arid environment.

The glass used in this study, which was exposed to seasonal precipitation as the main agent of weathering, was retrieved from a refuse site near the town of Cossack. Using Scanning Electron Microscopy (SEM), Energy Dispersive Spectroscopy (EDS), and X-Ray Diffractometry (XRD), the patina on the glass was analysed to ascertain its structure and chemistry, and to determine the effects of short-term burial (70–100 years) on the primary glass material in a tropical arid coastal environment in a carbonate quartz sand, and its exposure to seasonal precipitation.

Review of previous research on weathered glass

There has been a focus by other researchers on the depletion of the principal constituents of glass as a result of weathering, and on the species of minerals in the patina which are of exogenic origin. In this review, the various types of weathered glass are described in terms of type of glass, the setting of the weathered glass (*viz.*, whether in groundwater, sea water, or exposed to air), and weathering products.

The corrosion of glass has been documented since the 17th Century especially in Europe and the United States of America (Fearn *et al.* 2004). Some of the earliest research was carried out by Brewster who, in 1863, studied the diffraction effects (iridescence) arising from thin layers in a weathered crust on glass from the ancient city of Ninevah, located on the eastern bank of the Tigris River in Iraq (formerly Assyria). Newton (1971) cites Brewster's contemporary, Hausmann who, in 1856, conducted quantitative analyses of weathered crusts of the original glass from Ninevah and concluded that the crust was hydrated and that the alkalis, which had been essential ingredients in the glass, had been replaced by water, and that other metals such as iron, calcium and magnesium had been picked up from the environment.

A century later, Brill (1961) also focussed on the layers (laminae) in weathering crusts on ancient glass from Sardis, Turkey (buried sometime between the late 3rd century and the early 7th century), postulating that the laminae reflected periodic or cyclic change (such as seasonal variations in temperature or alternating wet and dry seasons) which were imposed during the long time of exposure (Brill 1961; Brill & Hood 1961). Brill (1961) also proposed that dating of glass artefacts could be achieved by counting the laminae of the weathering crusts on glass buried for many centuries. Though not accepted by some (*e.g.*, Newton 1966; Pollard & Heron 1996), this notion nonetheless had the potential to provide a chronometric method for archaeologists for whom the dating of glass artefacts was problematic.

Newton (1976), in a study of the weathering of medieval glass, noted that "conditions of burial seem much more exacting than even the worst ravages of atmospheric weathering". Newton (1976) recorded that weathering seemed to cause some fundamental changes to glass, and that buried glass not infrequently had a multi-laminated crust on its surface. In a study of hundreds of pieces of medieval stained glass by Newton (1976), provided they had not been buried, no weathering crust was found with the exception of some Austrian stained glass, the crust on which was quite thick compared with the laminae on archaeological [*sic*] glass. Newton (1976) also described the anomaly of the weathering crust on 300 kg of glass excavated from a cullet heap at the glassworks site at Bagot's Park in Staffordshire, England (dated to about 1535 AD); one half of the glass showed a heavy, opaque weathering crust whilst the other half was transparent and uncrusted.

More recently, Cox & Ford (1989), using SEM, electron-probe analysis, X-Ray and electron diffraction, described the nature of glass decay processes from alkali-lime-silicate glasses which had corroded on the sea bed for approximately 240 years. The samples (fragments of glass containers) were retrieved from two in-shore shipwrecks, the first, the *Drottengin af Sverige*, which was wrecked off Lerwick Harbour (Shetland Islands) in 1745, and the second, the *Amsterdam*, which foundered off Hastings in 1749. The samples exhibited opaque corrosion crusts which were between 0.2 mm and 0.5 mm thick, had become coloured, and were extremely fragile. Cox & Ford (1989) found that leaching and dissolution of glass networks had occurred. Corrosion crusts comprising regular discrete layers (or laminae) were formed through reprecipitation, and were depleted of calcium and magnesium, while aluminium was concentrated through the crusts and silicon was enriched at the glass-corrosion interface (Cox & Ford 1989).

Cox & Ford (1993) also examined the long-term corrosion of glass by groundwater. The samples of glass used in that study were excavated from several sites in the United Kingdom, (*viz.*, Eltham Palace, Kent; Rievaulx Abbey, North Yorkshire; Stamford Castle, Lincolnshire; and Wroxeter, Shropshire). The samples were corroded soda glass and potash glass which had been exposed to groundwater for between 350 years up to 1650 years. The corrosion crusts varied in thickness, colour, and uniformity of corrosion within and between samples. Cox & Ford's (1993) research showed that the surface layers on all samples had been depleted (to varying extents) of their principal constituents, with the exception of Si, Al and Fe. They identified deposits of calcite, calcium phosphate and manganese-rich minerals occurring within the crusts which were largely of exogenic origin, and that the geochemistry of the local groundwater played an important role in determining the chemistry of the weathering crusts.

Garcia-Valles *et al.* (2003) examined medieval stained glass from three restoration works to characterise glass decay. The medieval stained glass (from the 13th to 15th centuries) was from the Santa Maria del Mar and the Pedralbes Monastery church in Barcelona, and the Tarragon Cathedral in the northwestern Mediterranean area. The glasses were of two types: an Na-rich type and a K-Ca-rich type. Their research showed that Na-rich type glass did not weather (due to high silica content around 60% by weight), but the K-Ca-rich type of glass exhibited decay in the form of destructive (micro- and meso-pitting), and constructive (patina and microcrust) glass surfaces (Garcia-Valles 2003). The stained glass used in the study of Garcia-Valles *et al.* (2003) adds a level of chemical complication to the decay processes and the decay products that are not present in simple clear glass, therefore their results may not be directly comparable to this study. However, the results of Garcia-Valles *et al.* (2003) are useful in that they identify some of the chemical processes in the weathering of glass.

To date there have been no studies of the weathering of glass buried in calcareous quartz coastal dune sand in a tropical arid climate.

A summary of the features of weathered glass is presented in Table 1.

Current ideas of patina-forming processes

Patination occurs as a result of weathering processes acting on the surface of natural materials which include volcanic glass (obsidian) and rocks, and on glass artefacts. Maloney (1968) notes that pure silica is attacked by alkaline solutions, also noting that common glasses of soda-lime-silica composition "contain the seeds of their own chemical destruction" and, when it is exposed to water, a silica-rich surface layer [patina] develops on the surface of the glass.

Jackson (1997) notes that with obsidian (a volcanic glass, usually of rhyolitic composition), hydration rims are sometimes present in obsidian artefacts or Holocene volcanic glass.

Desert varnish (synonyms: desert crust; desert lacquer; desert patina; desert rind; rock varnish) is a possible type of patina less than 500 μm thick, often characterized by ultra-thin laminae. Desert varnish is found most frequently on rocks (sedimentary, igneous, or metamorphic rocks) with stable surfaces, in arid environments (Jackson 1997; Krinsley *et al.* 1998). It is composed of a thin coating of ferromanganese oxides, clay minerals, and trace elements (Krinsley *et al.* 1998). The mechanisms leading to desert varnish formation are

Table 1

Summary of types of glass, setting, and weathering products

Type of glass	Setting	Weathering products
ancient glass (Brewster 1863; Newton 1971 citing Hausmann (1856); typically high soda glass (Newton 1876)	excavated from Ninevah (Iraq), located on the eastern bank of the Tigris River	thin layers of weathered crust; diffraction effects (iridescence) noted
ancient glass (Brill 1961; Brill & Hood 1961); composition not described	excavated from Sardis, Turkey; glass buried for about 1600 years	weathering crust comprised of 1582 laminae
waste glass (Newton 1976); composition not described	excavated from a cullet heap at a glassworks site in Bagot's Park, Staffordshire, United Kingdom; exposed to groundwater for about 430 years	heavy, opaque weathering crust only on one half of the sample; the other half of the sample was transparent and uncrusted
medieval stained glass, typically high potash, high lime, and high magnesia (Newton 1976)	*in situ* stained glass in cathedrals and monasteries; exposed to humid atmosphere	no weathering crusts
alkali-lime-silicate glass (Cox & Ford 1989)	excavated from two shipwrecks (one located off Lerwick Harbour, Shetland Islands, the other off Hastings, United Kingdom); shipwrecks dated to 1745 and 1749 AD respectively	fragile opaque corrosion crusts between 0.2 mm and 0.5 mm thick arranged in regular, discrete layers;
soda and potash glass (Cox & Ford 1993)	excavated from several sites in the United Kingdom; various samples exposed to ground water for 350 up to 1650 years	corrosion crusts varying in thickness, colour, and uniformity of corrosion within and between samples
Na-rich and K-Ca-rich glass (Garcia-Valles *et al.* 2003)	*in situ* stained glass (13th–15th centuries) at Santa Maria del Mar and the Pedralbes Monastery church, Barcelona, and Tarragona Cathedral, north-western Mediterranean area.	glass decay in the form of destructive (micro- and meso-pitting) and constructive (patina and microcrust) glass surfaces. In the case of the Mediterranean medieval stained glasses, development of generalised corrosion and associated thick crusts are absent.

not completely understood, but it is postulated by some researchers to be the product of both abiotic and biotic processes (Krumbein & Jens 1981; Krinsley *et al.* 1998). Jackson (1997) cites that it is caused by exudation of mineralized solutions from within and deposition by evaporation on the surface [of the rock]. Garvie *et al.* (2008), on the other hand, disagree, describing desert varnish as neither a weathering rind, nor patina, but a unique subaerial authigenic sediment that forms under continuing adjustment to changing environmental conditions. As such, Garvie *et al.* (2008) would consider desert varnish not to be alteration *in situ*, but addition of microlayers of sediment and authigenic material.

Glass as the parent material to weathering crusts and patina

The composition of glass, particularly common, present-day commercial glasses, varies depending on the application for which the glass is intended. For example, fused silica, which is quite shock resistant, is > 99.5% SiO_2. Borosilicate, a glass that is thermally shock- and chemically-resistant, is composed of 81% SiO_2, 3.5% Na_2O, 2.5% Al_2O_3 and 13% B_2O_3. Soda-lime glasses, which are durable and are used for containers, have a composition of 74% SiO_2, 16% Na_2O, 5% CaO, 1% Al_2O_3, with 4MgO (Callister 1991). Most commercial glasses are referred to as silica-soda-lime glasses because the main constituents are silica (in the manufacturing of glass, derived from quartz sand), soda ash (Na_2CO_3) and limestone ($CaCO_3$) [Callister 1991]. The main difference between current industrial glass and historic glass is the relative greater proportion of flux in historic glass which was made at the expense of silica but which enhances chemical weakness of the glass with respect to corrosion (Garcia-Valles *et al.* 2003).

The composition of ancient glass varies markedly from present-day glass. Newton (1976) reports that ancient glass (*e.g.*, Roman glass) was typically high soda (11.99–23.73% Na_2O), low potash (0.15–3.29% K_2O), moderate lime (4.83–9.14% CaO), and low magnesia (0.08–2.20% MgO). By the 12th to 14th centuries, the composition of glass had changed quite considerably being low soda, high potash, high lime, and high magnesia; the high lime content gave the glass greater durability (Newton 1976).

Materials and methods – this study

In 2005, Alistair Paterson from the Centre for Archaeology at The University of Western Australia provided three pieces of glass from an historical archaeological site at Cossack, collected either from the surface, or from within the upper 5 cm of the soil, as part of an archaeological surface survey (Paterson 2003). These glass fragments form the basis for this study, however, to obtain supplementary information, I visited the Cossack archaeological site to ascertain the nature of the environmental setting where the glass was found. The historic glass from the Cossack refuse site, comprising two pieces of flat glass and one piece of medicine bottle glass, are soda-lime-silica glasses.

Field work

The refuse site where the glass was found was visited to determine the nature of the terrain, the type of sand or soil that the glass was buried in, and the proximity of the water table to the ground surface (to determine whether the weathering of the glass was a subaerial, vadose zone, or phreatic zone process), and to determine the types of natural processes that are operating in the area (*e.g.*, aeolian activity, rain infiltration, faunal and vegetation bioturbation). Three randomly-located samples of sand were collected for laboratory processing.

Laboratory studies

In the laboratory, the glass with patina was washed with distilled water to free it of any dust (derived from its period of burial in the sand), that may have been adhering to its surface. When dry it was examined under stereoscopic binocular microscope to describe its appearance, extent of patina coverage, and relative thickness. To determine whether the patina was calcareous, a fragment of each of the three glass samples was tested for calcium carbonate by placing a drop of 10% HCl on a portion of the patina while examining it under a stereoscopic binocular microscope.

The glass from Cossack was also examined and analysed using SEM and EDS at the CSIRO facilities at Kensington, Western Australia. A fragment of each of the glass samples, broken transversely to expose the glass-to-patina contact, was coated with carbon. The edge of the broken glass, transverse to the plane of the glass, was examined under high resolution by SEM to obtain images 10–200 μm in size. Image fields of view 100–200 μm in size also were obtained using back-scattered electron emissions (BSE) in order, firstly, to map the distribution of average atomic number which was used as a surrogate to determine the consistency of element distribution, and hence consistency of the distribution of micro-structure types, and secondly, to map the distribution of selected elements (specifically Ca, Mg, Al, and Si). During the SEM, within each SEM field of view some 10–50 μm across, the sample was also analysed by EDS to quantitatively determine elemental composition; routine spot analyses of areas 1–3 μm in size were carried out, with selection of the area of analysis based on the heterogeneity of the SEM image, or heterogeneity of the BSE field, on micro-structural and/or textural contrast, and on micro-topography.

Where Ca or Al was present in abundance in the patina compared to the parent glass, with the implication that calcium carbonate or a clay mineral was present, some of the patina was scraped off and the sample analysed by XRD.

The glass samples from Cossack, each comprised of the essential ingredients soda-lime-silica, used in this study were:

- Sample A1 = flat glass 1.4 mm thick
- Sample A2 = flat glass 1.4 mm thick
- Sample A3 = bottle glass (medicine flat) ~ 3.6 mm thick

The EDS results are presented in two forms: as raw data of the main constituent elements of Si, Ca, Na, K, Al, and Fe (as cps, *i.e.*, counts per second) [Table 2], and as transformed data of the same elements against a normalised Si content (Table 3). The latter method highlights the relative depletion or enrichment of a given element against Si as a standard (*i.e.*, the relative proportion of the other elements compared to Si since Si is by far the most abundant element in the parent glass and the patina), and highlights the exogenic origin of some specific elements.

The sand in which the glass samples were buried is a calcareous quartz sand. The sand also was examined under stereoscopic binocular microscope to ascertain the nature of the surface of the carbonate grains. Shell grit from a modern nearby mid-tidal flat also was similarly examined for comparative purposes. Subsamples of the three randomly-collected sand samples were dry-sieved at 1 ϕ intervals to characterise their grainsize. The < 63 μm fraction, derived from the sieving, was analyzed by XRD to determine its mineral composition. Subsamples of the three randomly-collected sand samples also were subjected to acid digestion with dilute HCl to determine the % carbonate in the sediment.

The study area

Cossack is located 20° 40' 43" S 117° 11' 20" E in the Pilbara region of Western Australia on the shore of Butcher Inlet near the mouth of the Harding River (Fig. 1A). The town was founded in 1863 (Lorblanchet & Jones 1979), and was a colonial town in Western Australia in the middle to late 19th century. Cossack was the first port in Western Australia, and between 1866 and the early 1890s it was the centre of the pearling industry (De La Rue 1979) in the State. The former Cossack settlement was located on a narrow spine or peninsula, underlain by Precambrian rock, elevated above the surrounding tidal flats, mangrove-vegetated flats, and salt marshes (Geological Survey of Western Australia 1979), or salt flats of Semeniuk (1986), and mantled by and flanked by calcareous quartz sand dunes, supratidal sand flats, and spits (Figs 1A, 1B and 1C). In this context, the refuse site is located partly on a calcareous quartz sand dune, and on a terrain of calcareous quartz supratidal sand flat and sand spit.

During its short history, Cossack was a small town with a population of only several hundred permanent residents at its peak in the 1890s, though the population fluctuated with the seasonal arrival and departure of the pearling boats at the beginning and end of the pearl-fishing season. The town went into decline when the pearling fleet moved to Broome in the early 1890s. In 1910 the prominence of the port further declined with the opening of the tram line to Port Samson, the new port for the region (De La Rue 1979). Cossack was a "ghost" town by the mid-1940s.

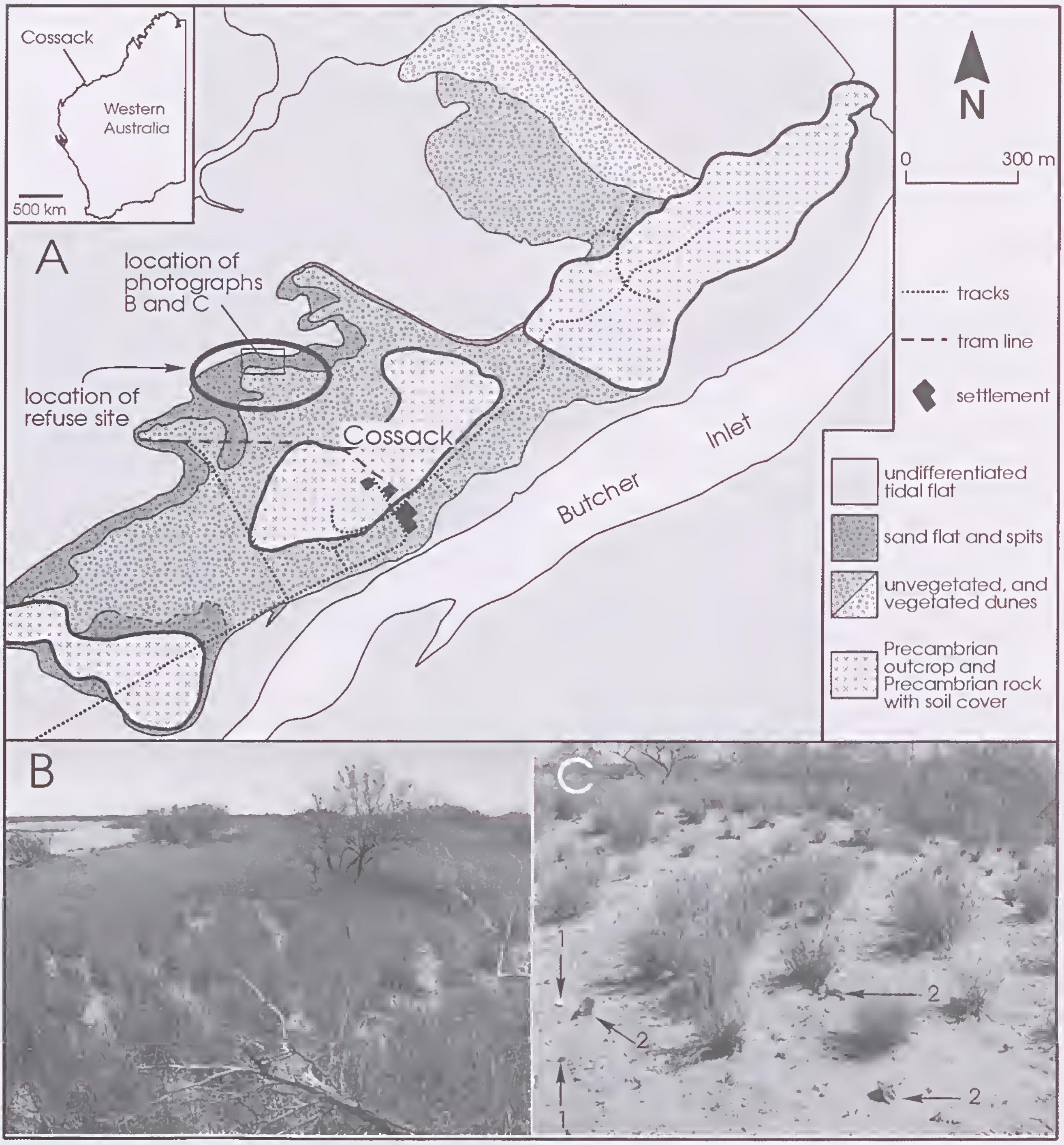
Cossack
Western Australia
500 km
A
location of photographs B and C
location of refuse site
Cossack
Butcher Inlet
N
0
300 m
tracks
tram line
settlement
undifferentiated tidal flat
sand flat and spits
unvegetated, and vegetated dunes
Precambrian outcrop and Precambrian rock with soil cover
B
C
1
2
2
2
1

Figure 1. Location of site. A. Map of the Cossack area showing landscape units, the location of the refuse site (as noted on Figure 4 of Paterson [2003]), and the location of photographs. B. Photograph of the sand flat adjoining the dune; tidal flat visible to left of photograph. C. Close-up of the surface of the sand flat that functioned as a midden site and then as a refuse site, showing shell (middens) scattered on the surface (arrow 1), and partly buried bottle fragments (arrow 2).

The climate of the Cossack area is tropical arid, with an annual average rainfall of 315 mm (Bureau of Meteorology 1973, 1975). Average summer temperatures range from a maximum of 36.5 °C and a minimum of 24.5 °C, with average winter temperatures ranging from a maximum of 25.5 °C and a minimum of 14.1 °C (Bureau of Meteorology 1973, 1975). Annual evaporation is ~ 3200 mm/pa (Bureau of Meteorology 1988). Cossack experiences summer rain with the highest rainfall occurring between January and March. The area also experiences strong, sand-shifting winds throughout the year (Semeniuk & Wurm 1987).

The refuse site is located 750 m north of Cossack town, and is located on a sand dune, supratidal sand-flat, and sand spit complex bordering a muddy tidal flat that occurs to the north of the spine or peninsula of Precambrian rock (Fig. 1A). The refuse site is composed of historic material comprising broken bottle glass, broken ceramic crockery, metal utensils, other domestic metal objects, and corrugated iron and other building materials, as well as Indigenous artefacts such as bottle-base fragments exhibiting flake scars, and accumulations of *Anadara granosa* (Lamprell & Healy 1998), broken *Telescopium telescopium* and *Terebralia palustris* (Abbot & Dance 2000) [all three species being a food source in that area], and *Melo amphora* (Wilson & Gillett 1974). As a sand dune and sand spit complex, the surface of the terrain of the refuse site is well above the water table (> 1 m above the water table); thus the deposits of broken glass are not located in the phreatic zone but in the subaerial and vadose zones. The surface of the refuse site is subject to strong winds such that the assemblage of historic glass has been variably covered and uncovered by ephemeral sand veneers, and additionally there is evidence that burrowing macrofauna have exhumed and buried the glass artefacts. As such, through the agencies of wind and fauna, the glass artefacts have been alternately covered in sand and exhumed, *i.e.*, they have been alternately in the vadose zone and subaerial zone.

A broken cylindrical bottle, *in situ* in the field, partly buried by sand, shows the relationship between patina and its burial in sand (Fig. 2B). The curved sand-to-glass interface has resulted in a curved margin to the developing patina, and progressive exposure of the bottle by wind erosion has resulted in curving parallel bands of the edges of the patina as it accreted and at the same time the bottle was progressively exposed.

From their setting, all three samples of glass from the refuse site at Cossack are estimated to have been buried for between 70–100 years.

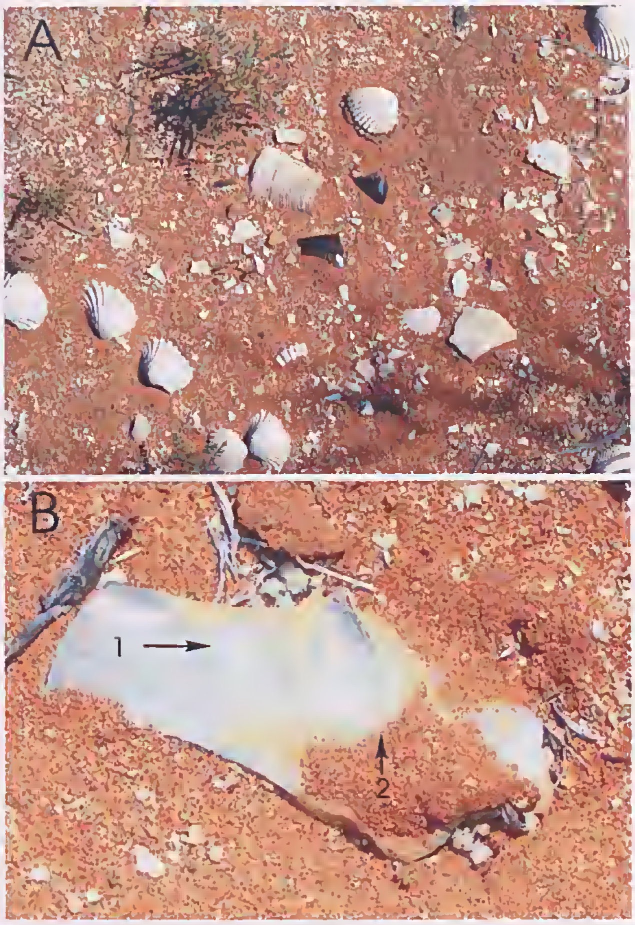

Figure 2. Photographs of the surface of the refuse site. Both photographs show the nature of the orange sand that is typical of coastal sands in this arid environment. A. Surface littered with *Anadara granosa*, partly buried, broken *Telescopium telescopium*, and partly buried dark bottle fragments. B. Close-up of a bottle fragment, *in situ* in the field, partly buried by sand. Edges of patina, in curving parallel bands, are evident on this bottle surface. Arrow 1 shows the limit of patination on the bottle. Arrow 2 shows a curved interface of sand on glass, where the cylindrically curved body of the bottle was buried. The curved sand-to-glass interface has resulted in a curved margin to the patina, and progressive exposure of the bottle has resulted in curving parallel bands of the edges of the accreting patina.

Results

Field results

In the field, the historic glass fragments are strewn across the surface of, or buried to shallow depth in the sub-surface of the sand dune, sand flat, and sand spit (Figs 1C and 2A). Evidence of burial and exhumation of historic glass by wind (as noted above) is shown by lines of patina on wind-exposed glass. (Fig. 2B).

Laboratory results

The sediments and soils on which the refuse site is located are comprised of medium and fine calcareous quartz sand in which the carbonate component is shell, mainly as fragments. The carbonate content in the sand varies between 10% and 15%. Coarse sand-sized shell fragments and shell gravel in the sediment and soils had surfaces that were predominantly corroded in comparison to shell grit from modern tidal flats.

Viewed under a stereoscopic binocular microscope, each of the samples of glass showed the patina to be present on both sides of the glass fragments, however, the patina was of a different thickness on one side of the glass compared with the other; the patina also coated the old broken edges. The upper surface of the patina generally appeared flat, though locally there were surface, low-amplitude undulations. The patina appeared relatively uniform in thickness on a given surface, and although it generally covered the glass, it was not uniform in extent – while dominantly covering the glass surface, there were patches where it was absent, or patches where it was more thinly developed. Where the patina was thin, the pitting on the parent glass surface was evident. The patina appeared to be a mosaic of overlapping plates or flakes, and the surface of the patina locally was undulating. There also were patches of closely-spaced "micro-vesicles" (see later) on the surface.

Wetting the surface of the patina with a drop of water showed that it was porous and permeable, with the water dispersing rapidly throughout the patina by capillary action along lamination interfaces and micro-cavities (this observation will have implications for pellicular water interactions with the patina and the parent glass). The patina was milky white (with local iridescence) appearing as an encrustation on the glass surface.

The testing of patina by dilute HCl showed effervescence in all samples, and hence the presence of calcium carbonate. However, the treatment of the patina with dilute HCl did not remove all of the encrustation – the residue remaining on the glass surface was a transparent to translucent, very finely-laminated crust (presumably of insoluble silica). The species of calcium carbonate within the patina (determined by XRD) are calcite and aragonite.

XRD results of the < 63 µm fraction show it to be composed of the following: the clay mineral kaolinite; micas biotite and clinochlore; feldspars as ordered calcian albite, disordered calcian albite, disordered anorthoclase, sodian anorthite, anorthite, and orthoclase; carbonates as aragonite, calcite, and dolomite; and other minerals such as quartz, geothite, haematite, talc, cordierite, ferroan cordierite, and rutile. Notwithstanding that these minerals have variable rates of weathering, and therefore different potential rates of availability of the metals as cations, the list provides an indication of the cations that may be mobilised during weathering. It also provides a list of the specific minerals (with their diagnostic cation signatures) that potentially can be incorporated into the patina. From a consideration of the chemistry of these minerals (Sinkankas 1964; Deer *et al.* 1966), the metals that can therefore be expected to occur in the patina, either as part of the minerals incorporated into the patina, or as remobilised elements, are: Al, Ca, Fe, K, Mg, and Na.

Description of SEM images and EDS results

The images obtained by Scanning Electron Microscopy are presented in Figures 3–8, which show a variety of micro-structural features, and glass to patina relationships.

The SEM images and EDS of all samples show the parent glass to be structureless (massive) and compositionally uniform. EDS of the samples shows it to be a soda-lime-silica glass, with Ca and Na in moderate proportions relative to the silica which is dominant (Table 2).

Table 2

Results of selected element content by EDS of glass and patina for the 3 samples

Sample A1

Element	*Glass (cps)*	*Patina (cps)*
Si	56.0	62.0
Ca	13.0	11.0
Na	6.0	1.0
K	0.5	1.0
Al	1.0	4.0
Fe	0.2	0.5

Sample A2

Element	*Glass (cps)*	*Patina (cps)*
Si	175.0	105.0
Ca	35.0	55.0
Na	30.0	0.2
K	–	–
Al	–	0.6
Fe	–	0.1

Sample A3

Element	*Glass (cps)*	*Patina (cps)*
Si	160.0	106.0
Ca	30.0	20.0
Na	23.0	18.0
K	0.5	1.0
Al	–	trace to 6.0
Fe	–	trace

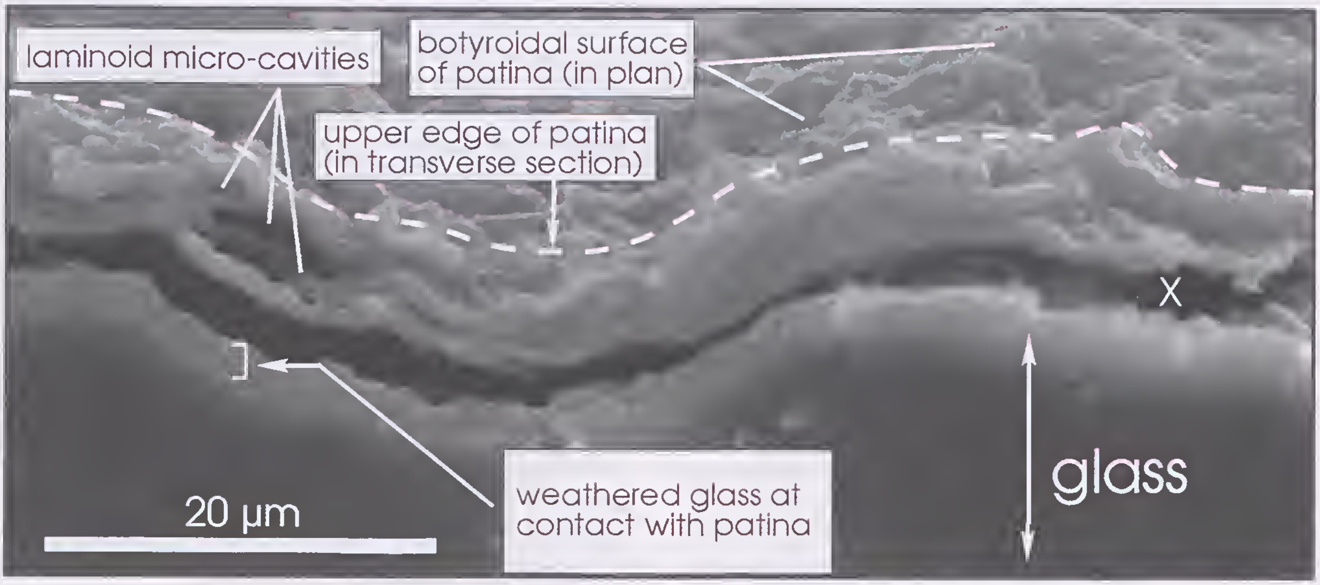
laminoid micro-cavities
botyroidal surface of patina (in plan)
upper edge of patina (in transverse section)
X
weathered glass at contact with patina
glass
20 µm

Figure 3. SEM image of a cross-sectional view of patina on glass (sample A1) showing undulating lamination and laminoid micro-cavities. The surface of the patina is botryoidal. The black zone (marked X) between the glass and the patina is a separation crack formed during sample preparation.

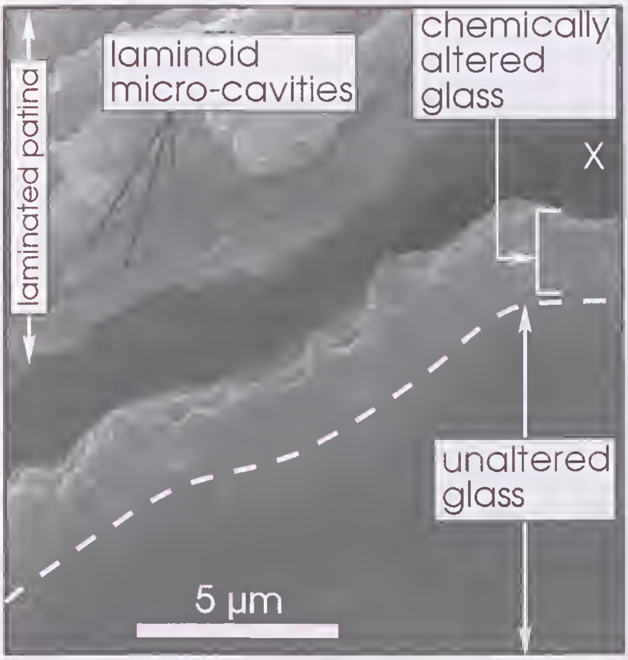

Figure 4. SEM image of a cross-sectional view of patina on glass (sample A1) showing details of features across the glass-to-patina interface. The image also shows a close-up of laminoid micro-cavities within the patina lamination. The black zone (marked X) between the glass and the patina is a separation crack formed during sample preparation.

The SEM images of the samples in transverse section show the patina to be a thinly-laminated crust (6–100 µm thick) on the glass surface. Depending on the glass sample examined, there are 5–12 laminae within the patina. The upper surface of the patina generally is botryoidal to undulating (Fig. 3). The lower contact of the laminated patina with the parent glass generally is sharp and irregular to scalloped. Also, there may be a zone of transition (5–100 µm thick) where the parent glass grades into the base of the patina through chemical alteration.

As will be described in detail later for each of the glass samples, the patina on the Cossack glass commonly contains micro-cavities. Two types are recognised (Figs 3, 6C and 8): 1) a lamination-parallel form that is platy, termed here "laminoid micro-cavity", that produces a laminoid micro-cavernous structure throughout the patina; and 2) another form that is more equant in shape, termed here "micro-vesicle", that produces a micro-vesicular structure in the patina. The laminoid micro-cavities tend to vary in size but range from 3–25 µm in length and from 0.2–1 µm in width in cross-sectional shape. The micro-vesicles tend to be 1–3 µm in diameter and are equant in cross-sectional shape.

In all patinas there are micro-unconformities where an undulating set of laminae is truncated by a later set of laminae (Figs 6B and 6C).

In plan, the SEM images show the patina may be micro-vesicular (Fig. 5A), and where it has been flaked off to expose the parent glass, the parent glass exhibits micro-pitting (or micro-etching) with individual micro-pits 1–20 µm in diameter and extending 5–10 µm into the glass (Figs 5A and 5B). Plan view images of the patina show a concentric pattern where the patina lamination follows the morphology of the pits (Fig. 5B). In transverse section, all samples show the contact between the parent glass and the patina to be a series of undulations, pits, and scallops where the glass has been corroded and there has been "invasion" by weathering products into the glass (Figs 5A, 5B, 6A, 6B, 6C, and 7). Figures 6A and 7 particularly well illustrate the corroded, pitted nature of the contact between parent glass and the overlying patina.

EDS results show that while the glass is dominated by the elements Si, Ca, and Na (typical soda-lime-silica glass), the patina is still dominated by Si but tends to be depleted of Na (though A3 is the exception). Ca may be depleted or enriched, though it is difficult to ascertain just from EDS results whether the Ca content is a residual from the parent glass, or exogenically derived. If present, K and Al are enriched in the patina relative to the parent glass.

All three glass samples provide good examples of the micro-structural, textural, and compositional characteristics of the patina, and the contact between it and the parent glass.

The patina in sample A1 is ~ 6 mm thick, and has 5 sub-parallel laminae (Fig. 3). There is minor compositional layering between laminae, with variation in content of Al, K, Fe and Na. The surface of the patina is botryoidal (Fig. 3). The lamination is undulating, with undulations subparallel to each other and parallel to the patina-glass contact. The parent glass along this contact is not flat, but appears pitted, and the undulations in the patina appear to perpetuate the micro-topography of the corroded parent glass. There are numerous laminoid micro-cavities varying between 3–11 µm in length and between 0.25–0.75 µm in thickness in cross-section, parallel to the lamination, and micro-vesicles averaging ~ 2 µm in diameter between and within the lamination (Figs 3 and 4). The EDS results for sample A1, that have been normalised with respect to Si, show that in the patina, Ca is relatively mildly depleted, Na is markedly depleted, K is relatively enriched, Al is markedly enriched, and that Fe also is enriched (Table 3). These EDS results show endogenic depletion and exogenic enrichment of the different elements, as will be discussed later.

The patina in sample A2 shows thick development on one side of the glass and thin development on the other. The thin side was examined by SEM. The thick side was analysed by XRD. The patina examined by SEM is up to ~ 30 µm thick, and has 10 sub-parallel laminae (Fig. 6), with minor inter-laminae compositional layering showing variation in Al. The lamination is undulating (Fig. 6C), similar to sample A1, but here the undulations do not always follow the irregularities of the topography of the parent glass. There also are numerous laminoid micro-cavities varying between 7–16 µm in length and between 0.4–1 µm in thickness, appearing in cross-section sub-parallel to the lamination, and micro-vesicles averaging ~ 3 µm in diameter between and within the lamination. The small micro-vesicles in fact dominate the structure of the patina (Fig. 6C). When the EDS results have been normalised with respect to Si, they show that

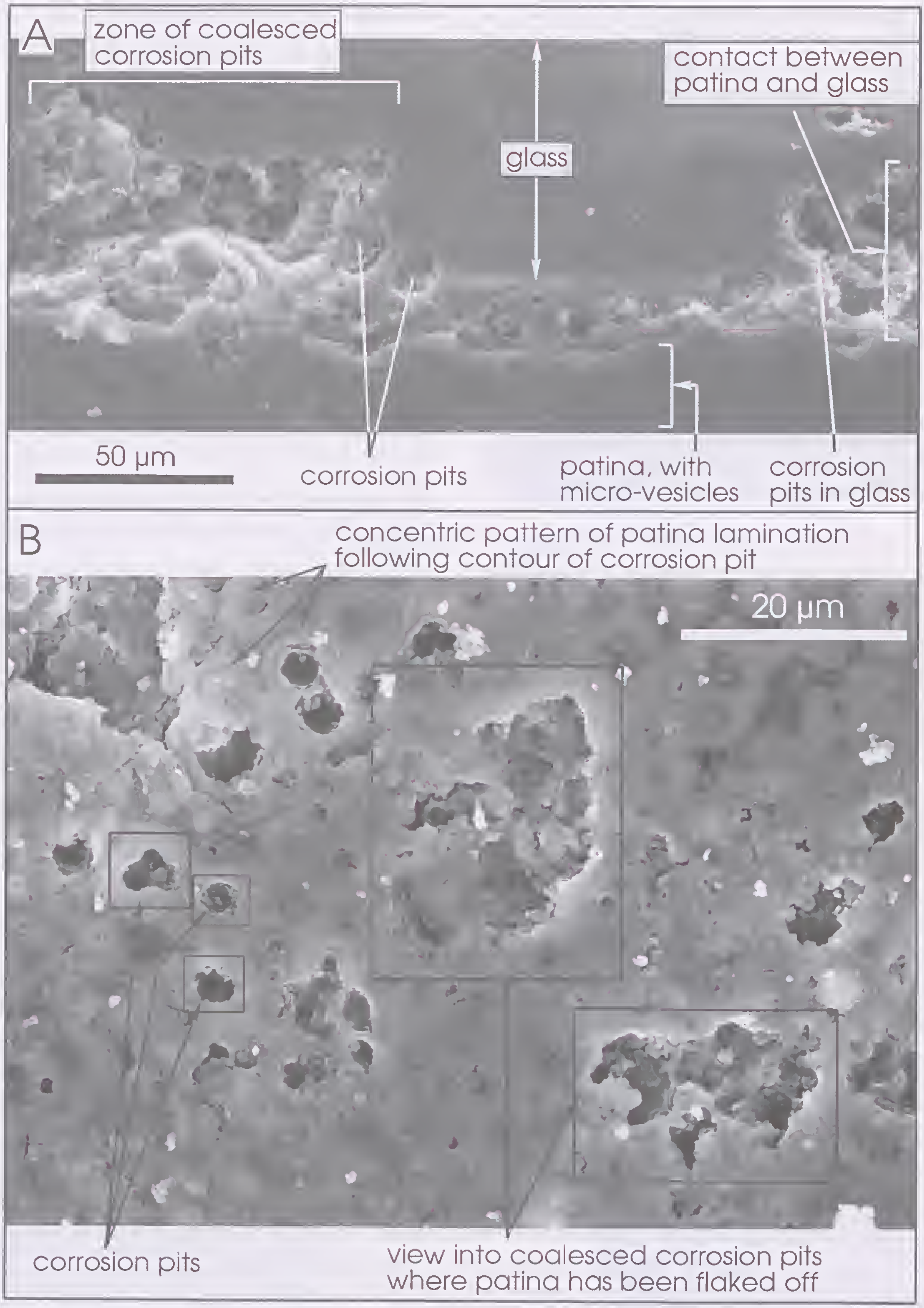
A
zone of coalesced corrosion pits
glass
contact between patina and glass
50 µm
corrosion pits
patina, with micro-vesicles
corrosion pits in glass
B
concentric pattern of patina lamination following contour of corrosion pit
20 µm
corrosion pits
view into coalesced corrosion pits where patina has been flaked off

Figure 5. SEM images of a plan view of patina on glass (sample A1). A. Image shows details of features across the glass-to-patina interface at the edge of the patina crust, where it has been flaked off. The patina has micro-vesicles. The glass is structureless. The contact of the patina on glass is marked by a zone of corrosion pits and coalesced corrosion pits. B. Image shows abundance of corrosion pits and coalesced corrosion pits, and the concentric pattern of the laminated patina where it has followed the morphology of the pits.

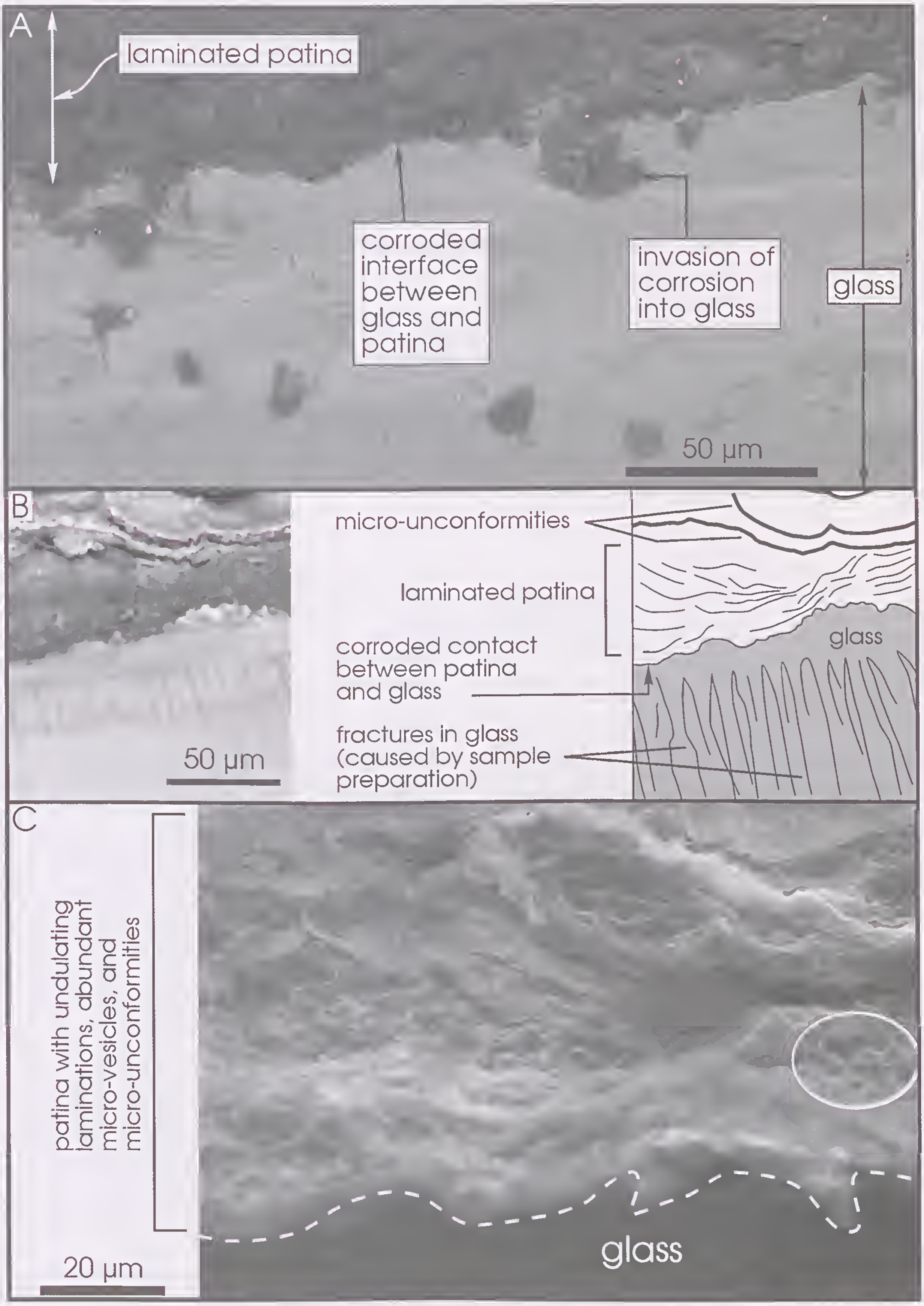
A
laminated patina
corroded interface between glass and patina
invasion of corrosion into glass
glass
50 μm
B
micro-unconformities
laminated patina
corroded contact between patina and glass
glass
fractures in glass (caused by sample preparation)
50 μm
C
patina with undulating laminations, abundant micro-vesicles, and micro-unconformities
glass
20 μm

Figure 6. SEM images of a cross-sectional view of patina on glass (sample A2). A. Image shows structureless glass, the corroded interface with the patina, the invasion of corrosion into the glass, and the laminated patina. B. SEM image and annotated line diagram showing corroded contact between glass and patina, undulating lamination in the patina, and micro-unconformities. C. Undulating lamination in the patina, and an abundance of micro-vesicles (one set is circled).

Table 3

Results of selected element content by EDS normalised with respect to Si

Sample A1

Element	*Glass*	*Patina*	*Comments*
Si	100.00	100.00	
Ca	23.21	17.74	Ca relatively mildly depleted in patina
Na	10.71	1.61	Na markedly depleted in patina
K	0.89	1.61	K relatively enriched (because of imported clay minerals)
Al	1.79	6.45	Al markedly enriched (because of imported clay minerals)
Fe	0.36	0.81	Fe enriched (because of imported dust)

Sample A2

Element	*Glass*	*Patina*	*Comments*
Si	100.00	100.00	
Ca	20.00	52.38	Ca markedly enriched in patina
Na	17.14	0.19	Na markedly depleted in patina
K	–	–	
Al	–	0.57	Al markedly enriched (because of imported clay minerals)
Fe	–	0.10	Fe mildly enriched (because of imported dust)

Sample A3

Element	*Glass*	*Patina*	*Comments*
Si	100.00	100.00	
Ca	18.75	18.87	no change in relative Ca content
Na	14.38	16.98	more or less the same Na content
K	0.31	0.94	K relatively enriched in patina
Al	–	trace to 5.66	
Fe	–	trace	

in the patina Al is enriched, Ca is markedly enriched, Na is markedly depleted, and that Fe is mildly enriched (Table 3). Again, these EDS results show endogenic depletion and exogenic enrichment of the different elements, as will be discussed later. The EDS results also show that there is compositional layering of Al.

The patina in sample A3 is ~ 50 µm thick, and has 12 finely-spaced, sub-parallel (mainly planar) laminae (Fig. 8). There is minor compositional layering between laminae, with variation in content of Al, K Fe, and Na. The lamination is generally parallel to the flat surface of the glass, *i.e.*, it is not undulating. There are numerous small cavities in the patina parallel to the lamination; these are laminoid micro-cavities varying between 6.5–24.5 µm in length and between 0.2–0.4 µm in thickness in cross-section (Fig. 8), and micro-vesicles averaging ~ 0.75 µm in diameter sub-parallel to the lamination. When the EDS results have been normalised with respect to Si, they show no change in relative Ca content, Na content remains more or less the same, and K is relatively enriched (Table 3). Trace amounts of Al and Fe appear in the patina. These EDS results show exogenic enrichment of K, Al and Fe, as will be discussed later.

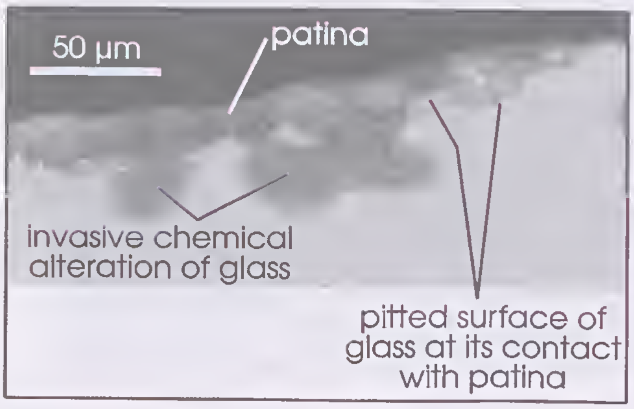
50 µm
patina
invasive chemical alteration of glass
pitted surface of glass at its contact with patina

Figure 7. SEM image of a cross-sectional view of patina on glass (sample A2) showing invasive chemical alteration of the parent glass, and the pitted surface of glass at its contact with patina.

Discussion and conclusions

The EDS results corroborate that chemically the parent glass is Na-Ca-Si. The elemental composition of the glass (and largely free or depauperate of Al and Fe) and its structureless (massive) nature provides a baseline to contrast the composition of the patina, and also an indication of what elements may be endogenic or exogenic in the patina.

Chemically, while the patina is dominated by silica, it shows both endogenic and exogenic elements. The definite endogenic element is Si. Although Na and some K are present in the glass and in the patina, it is not unequivocal that these latter elements have been derived endogenically from the weathering of the glass, or

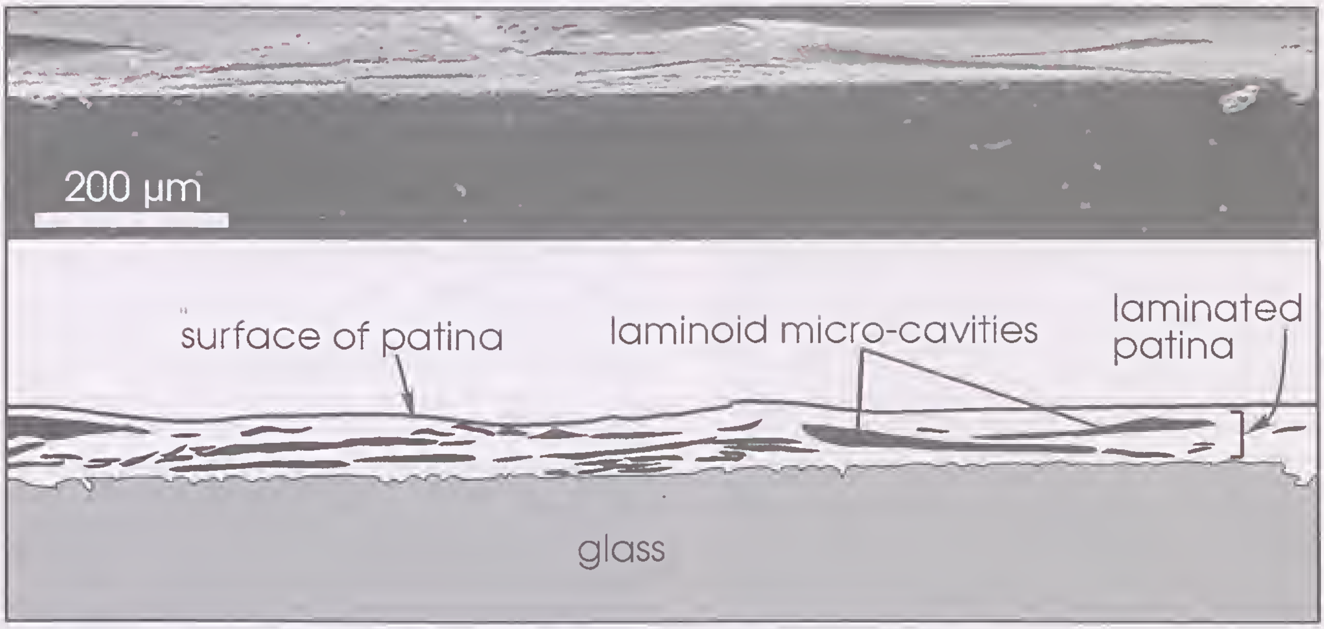

Figure 8. SEM image and annotated line diagram of a cross-sectional view of patina on glass (sample A3) showing laminated patina, and laminoid micro-cavities.

whether they have been introduced exogenically as a part of the interaction of patina with the Na-rich and K-rich components in the < 63 µm mineral fraction in the sand, given that Na and K are present in the parent glass *and* in the exogenic minerals. Na also could have been contributed to the patina as precipitation of halite, as the sand (in which the glass was buried) is in a coastal environment where wind-fall can bring in sea salt; rain also can be charged with sea salt. The concentration in the patina of Al, Fe, some Ca (as $CaCO_3$), and some K, as compared to their occurrence in the parent glass, suggests exogenic enrichment. How these elements occur within the patina, whether as elements bonded within the silica network, or as infiltrated minerals incorporated into and between the layers of silica, is not known. The EDS element map of Al shows that this element is compositionally layered within the lamination of the patina, and therefore its incorporation into the patina was in phase with the accretion of the patina lamination.

Of the range of elements available as leachates from the < 63 µm mineral fraction, and the dust-sized minerals themselves available to be incorporated as particles in the patina, only Al and Fe appear in the patina to any significant extent, and K appears in the patina moderately enriched. Probably the Al and K reflect the clay minerals and feldspar grains that were delivered as dust to the site in the Pilbara coastal region, and washed in by vadose processes or involved in the wetting and drying of sand grains and glass by dew-related processes. Some of the Na may also be exogenic as it may have a source from the breakdown of feldspars. Fe appears in all samples of patina at Cossack, and is exogenic. This is not unexpected as Fe-rich dust, containing geothite and haematite, is the hallmark of red dust in the general Pilbara region.

The occurrence of Ca in the patina is problematic to interpret. Some may be endogenic (derived by weathering from the Ca in the parent glass), but some may be exogenic deriving from dissolution of carbonate grains in the sand. Interestingly, while EDS shows Ca-enrichment in the patina which signals the potential presence of a carbonate species, laminae of carbonate were not evident in the EDS images. However, XRD shows calcite and aragonite in the patina, indicating that while the parent glass is free of aragonite and calcite, both these mineral species have been precipitated (or perhaps even illuviated) onto and within the patina. Some of the Ca which has been detected by EDS also may be present as trace amounts of (Ca-bearing) feldspars incorporated into the patina, though XRD did not detect these mineral species in the patina. It is more probable that the Ca presence in the patina is due to the occurrence of aragonite and calcite laminae. The removal of carbonate minerals by dilute HCl in the laboratory changes the appearance of the patina from laminated and milky white (*i.e.*, interlayered silica and carbonate) to laminated transparent/translucent (*i.e.*, laminated silica without carbonate), indicating that carbonate minerals are part of the patina structure.

The local iridescence of the weathered glass is the result of light interacting (diffracting) with a finely-laminated silica in which there are lamination-parallel micro-cavities.

While the EDS and XRD analyses provide useful chemical and mineralogic information on the element content and their possible endogenicity or exogenicity, micro-structural and textural data are required to more fully interpret the processes that produce patina and its internal structures.

In contrast to the structureless (massive) glass, the patina is rich in micro-structures: it is laminated; the laminations may be undulating; there are micro-unconformities; and the patina exhibits laminoid micro-cavities and micro-vesicles. These micro-structures provide information on processes that have operated in the formation of the patina, though a full investigation of these processes and products is beyond the scope of this paper. However, in the first instance, the laminated micro-structure shows that patina is accretionary on (or into) the parent glass surface. With accretion, some of the exogenic cations (incorporated as elements into the silica of the patina, or incorporated as mineral particles) are interlayered with the lamination producing compositional layering.

The micro-structural relationship of patina to parent glass shows that the base of the patina is invasive (corrosive) downwards, producing pitting in its contact with the parent glass. This indicates dissolution along the contact, with the patina accreting at the expense of the parent glass. This invasive relationship downwards would imply that a major component of the accretion of laminae is directed inwards towards the parent glass. The flatness of the upper surface of one of the patinas suggests little upward accretion, however, the locally undulating upper surface of other patinas, and the mosaic nature of the crust suggest there has been at least some outward (upwards) accretion.

That the patina on the glass from Cossack is porous suggests that there is possibility of thorough wetting of material during the wet season, and the possibility that accretion is in fact in two directions: that towards the glass, and that outwards from the surface of the patina. However, with the interior surface of the patina interfacing with the metastable glass, it is more likely that the major part of the accretion is, in general, downwards into the glass.

Pellicular water has been documented as being asymmetrical on sand grains, forming "gravitational" structures (Muller 1971), or "pendant" structures (Blendinger 2004) on the lower surface of the grain. At Cossack, if the glass is not being rotated within the soil/sand profile (*e.g.*, by bioturbation), asymmetrical pellicular water interacting with metastable glass has the potential to form an asymmetric patina.

The micro-structures also suggest that accretion alternated with dissolution, resulting in micro-unconformities. Sets of laminae are truncated by solution, and then the solution-sculptured surface provided the foundation for later micro-accretionary processes. The undulations, as described earlier, appear to be accretionary perpetuation of the irregular contact of the parent glass with the patina. Other undulations are the accretionary perpetuation of laminae superimposed on a solution-corroded surface sculptured earlier on the patina. The micro-unconformities and diverse sets of undulating laminae suggest that the patina has been through alternate phases of surface dissolution and silica accretion.

As noted above, although EDS shows Ca-enrichment in the patina relative to the parent glass, which signals the possible presence of a carbonate species; distinct laminae of Ca layers (as calcium carbonate) were not evident in the EDS images. The lamination-parallel micro-cavities in the patina suggest that these cavities may represent former laminae of carbonate minerals, and that their dissolution created the lamination-parallel cavitation. That is, in an environment where the pellicular water alternates between carbonate dissolving (and silica precipitating) and carbonate precipitating (and silica dissolving), the calcite and aragonite laminae within the patina, precipitated during the evaporation phase of any remaining pellicular water during the hot summer, is dissolved during the wet season to leave intra-patina cavities.

The processes of patination on the glass from Cossack appear to involve solution and precipitation, vadose-zone illuviation, and accretion. There is solution of the parent glass, precipitation of silica as laminae in the patina, solution of carbonate minerals, and solution of earlier-formed patina. There is precipitation of silica as laminated patina and precipitation of aragonite and calcite. There is probable vadose-zone illuviation of fine-grained mineral particles into the evolving patina, and incorporation of these particles into the accreting patina.

However, the weathering of glass at Cossack to form the patina did not involve just the parent glass in its interaction with pellicular water, but also complex interactions with the particles of the fine-grained mineral components and their weathering products (leachates and precipitates) of the sediment in which it was buried. Metastable anthropogenic glass is particularly prone to chemical weathering when it is exposed to water (Maloney 1968), and weathering can be expected to take place, but this weathering will be particularly accelerated if the water which the glass comes in contact with is alkaline. Weathering of metastable anthropogenic glass may have taken place at a slower rate, for instance, if it were to have been buried in a quartz sand with mildly or moderately acidic groundwater or pellicular water. At Cossack, dissolution of carbonate grains in the sand by rainwater resulted in a mildly alkaline pellicular water which could more actively chemically attack the glass (see below).

The relationship of silica dissolution and precipitation, and carbonate dissolution and precipitation, particularly where both materials co-exist in the same sediment or rock, and when pore waters are alkaline or acidic, or alternating alkaline to acidic, has long been a focus of sedimentary geochemistry (Walker 1962; Sharma 1965). Silica dissolution and precipitation can be complicated, and can be influenced by pH, lime, other metal salts, and electrochemical coagulation, amongst other factors (Fanning & Pilson 1971; Potapov *et al.* 2005). Also, according to the geochemical studies, precipitation of silica from sea water is almost impossible by inorganic means because of its low concentration, so organic agents have been invoked to precipitate the silica (Correns 1950; Siever 1957; Krauskopf 1959). These issues are important because the weathering of anthropogenic glass in the calcareous quartz sand at Cossack is in a silica/carbonate dissolving/precipitating environment, and the principles involved in the type of geochemistry outlined above are applicable to the weathering of glass at Cossack. However, notwithstanding that biomediation and other hydrochemical factors can reverse and influence some general patterns of silica solution/precipitation and silica and carbonate chemical relationships, there is a generally-held notion that acidic waters are carbonate dissolving, and silica precipitating, and alkaline waters are silica dissolving and carbonate precipitating (Walker 1962; Sharma 1965; Southwick 1984; Kendrick 2002). If silica, as quartz, is susceptible to dissolution under alkaline conditions, metastable anthropogenic glass can be considered to be even more susceptible to dissolution under alkaline conditions.

In a setting such as the coastal sands at Cossack that receives annual rainfall in the summer, the pellicular water micro-environment, as discussed above, can be alternating in pH. The laboratory observations indicate that water disperses rapidly through the patina, suggesting that any solutes present in the pellicular water derived from the sand, from shell, from the < 63 μm fraction in the sand, from the patina, and from the glass itself, have the potential to be transferred to any location within the patina and could interact with laminations, inter-laminations, and micro-cavities in the patina.

The research carried out by Semeniuk (2007) on the coastal calcareous quartz sands and wetland calcilutites ($CaCO_3$ muds) in the Point Becher area provides information and insights into some of the rainwater-and-carbonate interactions that can occur in the vadose zone. Semeniuk (2007) found that while rainwater was weakly acidic, rain-derived pellicular water around calcareous sand grains in coastal dunes, de-ionised water used as pellicular water around calcareous sand grains in laboratory experiments, and rainwater infiltrating calcilutites, dissolved the calcium carbonate component of sediments. With dissolution of calcium carbonate, the pore waters became alkaline.

In the Cossack area, with the onset of rain, the pellicular water initially would be weakly acidic. In contact with carbonate grains, the pellicular water would corrode them (the corroded carbonate sand grains and shell in the sand enclosing the glass attest to this), and would become weakly alkaline. Once alkaline, the pellicular water would attack the glass, promoting dissolution and the other chemical processes involved in patination. When the pellicular water evaporates, it would leave behind a precipitate of carbonate minerals (either crusted on the patina, in the pore spaces of the patina, or along the contact of the patina and the parent glass). The next episode of rain would re-introduce weakly acidic meteoric water which would dissolve the carbonate grains in the sand (liberating more calcium carbonate in solution), *and* dissolve carbonate minerals within the patina. The formation, structures and chemistry of the patina reflects the history of the glass embedded in a calcareous quartz sand with an annually alternating hydrochemistry and acidity/alkalinity of pellicular water as outlined above. The pellicular water chemistry, however, is more complicated by virtue of the fact that the mineralogy of the < 63 μm fraction in the sand appears to play a part in the evolution of the patina through its dissolution and perhaps its illuviation.

All glasses elsewhere that have been studied to date have been weathered in different types of environments (under the sea, buried in soil in humid England, in groundwater-saturated soil, and exposed to a humid atmosphere in Europe). They have all shown differences in style of weathering in terms of structures and lamination compared to the Cossack samples. For example: 1. glass in groundwater-saturated soil resulted in the formation of morphological features such as parallel layers, hemispherical layers, zigzag banding, rotated bands, and plugs (Cox & Ford 1993); 2. glass buried in soil exhibited circular and parallel weathering layers, and plugs (Newton 1971); and 3. medieval stained glass exposed to atmospheric weathering contained such features as curved-branched, irregular micro-pitting (Garcia-Valles *et al.* 1993). In contrast, the glass buried in calcareous quartz sand at Cossack, in an arid environment, has weathered to form a patina that is laminated, with undulations in the laminae, and with micro-unconformities, micro-cavities and micro-vesicles, and calcite/aragonite in the structure. This indicates that it is probable that the environment of weathering can influence the micro-processes of weathering and hence result in different types of microstructures and mineralogy. Axiomatically, the results from one area, with its particular climate, soil, and hydrochemistry, cannot be transferred to other areas in terms of deducing processes, products, or age.

In the literature the main agent identified in the environment responsible for the weathering of glass is water (Brill 1961; Cox & Ford 1989, 1993), whether as groundwater, pellicular water, sea water or atmospheric water, and the geochemistry of that water in these different environments will determine which constituents will be depleted from the parent glass, the composition of the patina, and the rate of dissolution and accretion depending on the pH.

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Seed collection for revegetation: Guidelines for Western Australian flora

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Abstract

Current approaches to seed collection for revegetation tend to follow a precautionary principle that advocates the use of seed of 'local provenance' from geographically restricted areas. In many cases however, assigning 'local' seed collection areas for specific taxa is not possible due to a lack of available information regarding local adaptation and patterns of genetic variation, the possibility of hybridisation among genetically divergent populations, and the possibility of invasiveness or other ecological interactions. We suggest that strategies for determining appropriate seed collection areas should be based on a number of considerations including: the aim of the revegetation program, characteristics of the site requiring revegetation, known or inferred patterns of local adaptation and genetic differentiation, and the availability and quality of seed sources in taxa used for revegetation. We review the limited information available regarding patterns of local adaptation and the partitioning of genetic variation for plant species commonly used in revegetation in south-west Australia. We suggest that the presence of local adaptation and partitioning of genetic variation may be inferred by assessment of a number of species-specific traits, and that adherence to restricted seed collection areas may not be the most appropriate approach for seed collection strategies for all taxa particularly common widespread species often targeted in restoration programs. In some cases, an ecogeographic approach where seed is collected from a number of large healthy populations at collection sites matched for climatic, edaphic and other environmental variables at the restoration sites, with less consideration given to geographic distance between them, may be a more appropriate strategy for seed collection.

Key words: revegetation, seed collection, provenance, local adaptation, genetic differentiation

Introduction

Determining appropriate strategies for collecting seed is an important issue for revegetation programs. Current approaches regarding seed collection tend to follow a precautionary principle that advocates the use of seed of 'local provenance'. The term 'provenance' is frequently used simply to describe the geographic origin or source of specific genetic material and is often applied when variation is observed in morphological and physiological traits over a species natural range (Coates & Van Leeuwen 1996). More specifically 'local provenance' is applied to seed collected locally or of local origin although 'local' is often not clearly defined. Where it is defined strictly in terms of a geographic distance between source and restored populations it is generally applied to all plant species regardless of their biological attributes, breeding system, geographic distribution and demographics.

Traditionally, seed collection guidelines recommend seed for revegetation be collected from 'local provenance' material, or from natural populations as local as possible. These guidelines advocate initial small on-site seed collection areas that may be gradually extended to the next geographically closest viable populations if seed supply is limited (Mortlock 2000a). This approach is generally recommended in the absence of information on the distribution of genetic diversity, in particular that which may confer adaptation to local environmental conditions (Mortlock 2000a).

There are a number of reasons that this precautionary approach has been adopted. (i) It is assumed that material sourced from local populations will be best suited to a specific site, possessing local adaptation to climatic, edaphic, biotic and other environmental conditions. Such 'local provenance' material may have a 'home site advantage' with enhanced long term population adaptation, viability and survival (Coates & Van Leeuwen 1996; Joshi *et al.* 2001). Conversely, material that is not adapted to local conditions may display reduced survival, growth, reproduction, and long-term persistence at revegetation sites (Potts *et al.* 2003). (ii) Local provenance material is considered to reduce the risks of outbreeding depression arising from crosses between genetically divergent yet interfertile, introduced populations and local populations. Outbreeding depression, a significant reduction in offspring fitness that may be expressed over a number of generations, can lead to low population viability and a substantial decrease in the likelihood of population persistence (Rhymer & Simberloff 1996). (iii) Local provenance seed is also considered to prevent negative ecological interactions such as changes to breeding systems, invasiveness, displacement of the local form and changes to the surrounding community structure;

however the relative risks of such impacts will be species and site specific.

There is now some debate on the most appropriate strategy for selecting plant material for revegetation, and whether locally sourced material is always the most appropriate (Montalvo *et al.* 1997; Lesica & Allendorf 1999; Hufford & Mazer 2003; McKay *et al.* 2005; Broadhurst *et al.* 2008). Bussell and Hood (2006) suggest that the importance of achieving successful revegetation and maintaining ecosystem integrity should override issues of spatial proximity of seed sources and revegetation sites. Arguments against restrictive seed collection strategies stress that non local genetic material may not necessarily be maladapted (for example when local adaptation is not present), hybrid progeny of interfertile yet divergent populations do not always display outbreeding depression and maladapted alleles may be readily purged by selection, (leading to only a short term decrease in fitness). Indeed there are relatively few studies in plants that have clearly demonstrated outbreeding depression (Edmands 2007). A restrictive approach toward local seed collection areas may also result in seed that is inbred, has limited genetic diversity and lacks potential to respond to past or future environmental changes. Thus this precautionary approach may be suitable for some species targeted for restoration but for other species it may be unnecessary and even counter productive.

A range of factors should be assessed when making decisions on appropriate geographic scale of seed collection areas and deployment of material at revegetation sites, including the aim of the revegetation program, current and future aspects of the revegetation site, patterns of local adaptation and the partitioning of genetic variation in the species to be utilised, and the availability and quality of seed. We discuss each of these factors below and how they influence seed collection strategies with reference to the flora of south-west Western Australia that is commonly used for revegetation.

Aim of the revegetation program

Restoration and revegetation programs operate at varied geographic scales and are conducted with a range of goals. The goal of many early revegetation projects was the rapid restoration of degraded land achieved via the establishment of plants of only a few species, often exotics, with a high survival rate (Lesica & Allendorf 1999). Other revegetation goals include the provision of specific habitat, the prevention of invasion by exotics, the re-establishment of select ecological functions and the restoration of compositional biodiversity. These programs have raised awareness of the use of native species for revegetation. Some revegetation programs aim to restore populations of specific endangered species and focus necessarily on the reintroduction of only those species, often at small scales. However, the aim of many present day, often large scale, revegetation programs is the re-establishment of fully functional and compositionally biodiverse, self-sustaining ecosystems that persist well into the future (Coates & Van Leeuwen 1996; Lesica & Allendorf 1999). Each of the factors affecting the choice of seed collection strategy is discussed below in the context of these large scale revegetation programs.

Site characteristics

Lesica and Allendorf (1999) recommend that the degree of disturbance at a revegetation site, as well as its size and proximity to local populations, should be taken into consideration. The degree of disturbance at a revegetation site may vary from slight degradation to total transformation. If the severity of disturbance is low and the abiotic environment has not altered significantly, nearby populations should still be well adapted to the environmental and ecological conditions at the revegetation site and seed from these sources, if of suitable quality, may be a first choice for revegetation (Lesica & Allendorf 1999). Examples of these sites may be logged forests where post harvest treatments are minimal and where the soil structure remains intact.

At highly disturbed revegetation sites, environmental conditions may be significantly altered and completely novel compared to the original state. Where there have been large changes to edaphic and ecological conditions, locally sourced genetic material may no longer be well adapted to the site (Lesica & Allendorf 1999). Indeed, more diverse seed collections of varying genetic material may provide the higher levels of genetic variation required for adaptation, population survival and long-term population persistence. In highly disturbed sites, matching for environmental factors may be more critical for successful revegetation than simply minimising the geographic distance between seed source populations and the site requiring revegetation, and the 'coarse selective tuning' or 'habitat matching' approach of McKay and Christian *et al.* (2005) may be more appropriate. This advocates an ecogeographic approach to revegetation with seed lots comprised of a mixture of genotypes from climatically, edaphically and ecologically matched populations. This approach would limit the introduction of highly maladapted genotypes and still provide enough genetic variation within the restored populations for further adaptive 'fine tuning'. Examples of severely disturbed sites may include roadsides, ex-agricultural land, and mine sites where the topsoil has been removed.

The size and proximity of the revegetation site to local populations should also be considered as it influences the risk posed to local populations via the potential introduction of non-local material. This is particularly relevant when the area to be revegetated is large in comparison to nearby native vegetation (Lesica & Allendorf 1999), where the use of locally collected material will reduce the risk of hybridisation or negative ecological interactions between local and non-local populations. If the area to be regenerated is small or isolated, there is little chance locally adapted genotypes will be swamped out by introduced non-local material. If the site is highly disturbed and also small or isolated in area, the 'coarse selective tuning' approach, using material from more diverse seed collections may be the best approach (McKay *et al.* 2005).

There is general recognition that for survival over the short term, genetic variation within populations is often less critical than stochastic demographic, environmental and anthropogenic events at the revegetation site (Coates & Atkins 2001). These events are by definition difficult to predict. However, there are also likely to be long-term changes to future environmental conditions, such as those caused by climate change. While increased temperature and decreased rainfall are predicted for south-west Western Australia, some of these future changes are also likely to be unpredictable, and suggest that the use of material of diverse origins where genetic diversity is maximised will be an advantage for revegetation programs (Harris *et al.* 2006). Seed collection strategies that sample seed from an increased number of more widely sourced populations will maximise genetic variation and increase the likelihood of capturing adaptive genes required for future conditions. Such approaches to seed collection should provide greater opportunity for evolutionary development in revegetated populations thus increasing the chances of long-term population persistence and revegetation success.

Local adaptation

The presence of local adaptation is often proposed as one of the reasons for a restrictive or localised approach to seed collection areas. Local adaptation is best investigated using an approach that assesses quantitative ecologically important traits of heritable variation, and combines common garden studies, reciprocal transplant studies, and crossing experiments over a range of geographic distances. A limitation of these methods is that they are costly and time consuming and not likely to be conducted for a range of endemic taxa or for non-commercial species.

Some information on local adaptation is available for three tree species from the south-west forests. Assessment of provenance trials in Jarrah found evidence for adaptive variation in traits such as survival, stem diameter and growth rate between provenances from the northern jarrah forest, the southern jarrah forest, and the Swan Coastal Plain (Alcoa, unpublished data). Within the northern forest region adaptive variation was low although provenances from low rainfall sites on the eastern edge of the forest had poorer growth (O'Brien *et al.* 2007). This finding suggests an approach using regional seed collection areas with ecogeographic habitat matching for northern and southern populations. The difference in performance between Swan Coastal Plain and main forest provenances is also consistent with historic genetic differentiation between these provenances identified with molecular markers (Wheeler & Byrne 2006).

Provenance trials of Karri also showed little adaptive variation between major river catchments and little genetic differentiation was detected among catchments (Coates & Sokolowski 1989; Mazanec & Mason 1993). Some outlying populations exhibited slower growth that may indicate adaptive variation. These findings suggest that seed collection areas may be broadened beyond major river catchments to more regional collection areas although outlying populations should be treated separately. Similarly, little adaptive genetic variation was detected in a study comprising a number of populations of *Allocasuarina fraseriana* (O'Brien 2007) indicating that seed may be sourced at a regional scale.

Environmental factors such as climatic (*e.g.* temperature, day night cycles, light, rainfall probability, frost tolerance, germination temperatures) and edaphic conditions (*e.g.* soil texture, water holding capacity, chemical composition), as well as ecological processes (*e.g.* mycrorrhizal associations, pollinator abundance, seed dispersers), may vary across a landscape and contribute to local adaptation. Thus, consideration of these factors may also assist in defining seed collection strategies. Indeed, the establishment of seed collection areas based on broad ecological and geographical similarities between the seed collection site and the area undergoing revegetation has been recommended in the absence of more detailed data on patterns of local adaptation (Jones & Johnson 1998).

Genetic differentiation

Determinants and patterns of genetic variation

It has been suggested that population genetic approaches can be applied to defining provenance since genetic data can be obtained more rapidly and cost effectively than ecological and reciprocal transplant studies (Coates & Van Leeuwen 1996; Bussell *et al.* 2006). The patterns of genetic variation measured by molecular markers primarily reflect the impacts of past gene flow and genetic drift and are not necessarily correlated with the forces of selection that confer local adaptation (Reed & Frankham 2001; McKay *et al.* 2005). Despite their limitations, neutral genetic markers are potentially useful in describing possible evidence of local adaptation. They are used to indicate population genetic divergence due to restricted gene flow and as pointed out by Lynch (1996) significant molecular divergence provides strong evidence that adaptive divergence has the opportunity to occur but it is important to note that lack of any molecular divergence is likely to be uninformative. Such marker-based predictions of genetic variation should ideally be combined with field studies to confirm that genetic variation reflects adaptive variation.

For many native species, information about the partitioning of genetic variation among populations will not be available. However, some indication of the likely patterns of genetic variation may be obtained by assessment of a range of biogeographical, reproductive and species life history traits that have been shown to strongly influence gene flow and the subsequent partitioning of genetic variation among populations (Hamrick 1979; Hamrick & Godt 1996; Nybom 2004). Pollen and seed dispersal, in combination with the breeding system, have a major impact on patterns of genetic variation among plant populations (Hamrick 1979; Hamrick & Godt 1996). Species with high levels of gene flow through highly mobile pollinators or wind pollinated systems tend to have lower levels of genetic differentiation among populations than predominantly selfing species and species where the opportunity for pollen and seed dispersal is limited. Life history traits and life form can be good predictors of spatial scales of genetic variation, with trees and later successional stage long lived perennials generally having higher levels of gene flow than herbaceous, early successional stage annuals that tend to have restricted gene flow and high population differentiation (Hamrick 1979; Hamrick & Godt 1996; Nybom 2004). Thus, assessment of these traits may indicate the likely levels of genetic differentiation in the absence of specific information on the partitioning of variation.

Some generalisations can be made with regard to patterns of genetic variation in terms of the geographic distribution of species although there will always be exceptions. Species with widespread or regionally continuous distributions would be expected to have ample opportunity for gene flow and therefore little genetic differentiation between populations. In species with relatively low genetic differentiation local adaptation would be limited or occur over broad geographic distances and seed collection areas for revegetation may be extended to intermediate or regional ranges. The most obvious barriers to gene flow in widespread plant populations may be components of the physical environmental such as rivers, significant landforms and major edaphic differences. These physical barriers may cause genetic differentiation among populations and form boundaries for seed collection areas.

The dominant trees of the south-west forests are widely used in revegetation and are examples of species that occupy wide, virtually continuous, geographic distributions. Genetic studies in these dominant tree species do indicate little geographic partitioning of genetic variation throughout the main range (Coates & Sokolowski 1989; Coates *et al.* 2002; Wheeler *et al.* 2003; Wheeler & Byrne 2006; O'Brien 2007; O'Brien *et al.* 2007), suggesting that broad regional seed collection areas may be used for these species.

In contrast to species with continuous distributions, many common Western Australian shrub species that are used for revegetation have geographically widespread but naturally patchy distributions and exhibit low to moderate levels of genetic variation between populations (Byrne 1999; Hines & Byrne 2001; Broadhurst & Coates 2002; Byrne *et al.* 2003; Elliott & Byrne 2003; Broadhurst *et al.* 2004). The distribution of these species is related to the natural mosaic of habitats throughout much of the south west, although species with patchy distributions can also occur in the more continuous habitat of the forest ecosystems. Moderate levels of genetic structuring in such species may indicate the possibility of adaptive variation among populations. This suggests that germplasm for revegetation should consist of more localised seed sources when possible, although factors such as characteristics of the revegetation site and the quality of local seed sources should be also considered.

We note here that we are not considering other species of the south-west flora that are not generally targeted for revegetation as they are rare, have isolated populations or highly disjunct distributions. These species, and those occurring in highly fragmented environments, or where significant geographic barriers to gene flow occur, generally have high levels of genetic differentiation (Coates 2000, Byrne & Hopper 2008). Seed collections from these species may be for specialised restoration programs and reintroductions but would not be targeted for general revegetation.

Chromosome variation

Variation in chromosome number, ploidy level and chromosomal rearrangements may have an important influence on the expression of outbreeding depression through the development of chromosomal barriers to gene flow. In these cases crossing between chromosomally differentiated populations can result in seed abortion, partially or fully sterile progeny or hybrid breakdown in subsequent generations leading to restoration failure in the long term (Coates & James 1979; James & Hopper 1981). Complex cytoevolutionary patterns including polyploidy, chromosome number changes and other kinds of chromosomal rearrangements are evident in a number of species from south west Western Australian with extreme examples including *Stylidium crossocephalum* and *Isotoma petraea* (Coates 2000). Although there are relatively few species where such data is available if the presence of ploidy or chromosomal rearrangements is identified in a given taxon, it would be prudent for seed collections to be sourced from populations of the same chromosome type as those at the revegetation site.

Taxonomic considerations

It should be noted that the accurate identification of the correct taxonomic entities represents an essential first step in defining seed collection areas for revegetation. Many native species show high levels of morphological diversity across their range and the dynamic nature of taxonomy in Western Australian flora means species are often subject to taxonomic revision (see Gibson *et al.* 2007). The correct identification of populations of newly described subspecies and variants may be an issue for seed collection in species complexes with high levels of morphological variation such as many acacias, *e.g. A. browniana, A. pulchella,* and *A. saligna*. However, population identification in the field is often difficult as morphological differences used to distinguish subspecies or variants may only be present at certain times of the year and identification may be further hampered by variable juvenile growth forms, as is the case for *A. saligna* (Millar *et al.* 2008). Genetic studies in *A. saligna* have revealed high levels of genetic divergence between the subspecies (George *et al.* 2006; Millar *et al.* 2008) and specific local adaptation is likely. For species complexes such as these, seed collections should be treated separately, and seed should only be used within the natural range of that subspecies or variant. As suggested by Coates & Van Leeuwen (1996) a first step for seed collectors is to keep abreast of reviews of the relevant taxa to ensure accurate population identification.

Quality and availability of local seed sources

The availability and quality of seed sources are also important in making decisions on the appropriate geographic scale of seed collection areas and the subsequent deployment of material at revegetation sites. In most revegetation situations the quality of the seed source should be considered more important than sourcing from the nearest population. Seed collected over a range of populations covering a climatically,

Table 1

Factors to consider when determining appropriate seed collection strategies for flora of south-western Australian commonly used in revegetation.

Factor	Aspect	Scale	Effect on seed collection area and collection strategy
Aim of revegetation program	Highly specialised goals	–	May require specialised strategies
	Functional and compositional ecosystem restoration	–	Consider the factors below
Characteristics of revegetation site	Degree of disturbance	High	Broader, more diverse collections, attempt to habitat match collection and revegetation sites
		Low	Localised collections
	Size	Large	Localised collections
		Small	Broader collections may be used if required
	Proximity to native populations	Isolated	Broader collections may be used if required
		Nearby	Localised collections
	Future changes	Likely or unknown	Broader, more diverse collections, attempt to habitat match collection and revegetation sites
		Unlikely	Localised collections
Presence of local adaptation	Known	Present	Localised collections
		Not present	Broad to regional ecogeographic collections
	Unknown	–	Assess partitioning of genetic variation
Partitioning of genetic variation	Known	High divergence	Localised collections
		Low divergence	Broad to regional ecogeographic collections
	Unknown	–	Assess likely extent of gene flow
Likely extent of gene flow	Requires assessment of distribution, biogeography, life history traits, cytogenetics and taxonomy.	Extensive	Broad to regional ecogeographic collections
		Restricted	Localised collections
Availability and quality of local seed sources	Availability	Local sources available	Assess quality of seed sources
		Local sources not available	Broaden collection area
	Quality	Large healthy populations	Suitable for collection
		Small unhealthy populations	Not suitable for collection, broaden collection area

edaphically and environmentally matched regional scale that provides high levels of genetic diversity will almost always be more appropriate material for revegetation than seed collected from a restricted number of 'unhealthy', small or isolated populations on a local geographic scale.

Small local populations may also be unsuitable sites for collecting seed for revegetation due to genetic impoverishment. Small populations, especially those of recently reduced size, may be suffering from inbreeding depression due to the effects of increased mating among relatives (Edmands 2007). Germination may be reduced and progeny may display reduced growth and survival due to the accrual of deleterious recessive traits in seed collected from such populations. Small populations experiencing inbreeding may also exhibit low levels of seed production. For example, Yates *et al.* (2007) found a decline in seed production with decreasing population size in the bird pollinated shrub *Calothamnus quadrifidus* where populations produced at least 50% less seed per fruit than large populations. Harvesting of seed from such populations is likely to result in further reductions in seed set and population recruitment, and enhance inbreeding depression in the population.

Practical aspects of seed collection may need to be considered as there can be a number of problems associated with the collection of geographically local seed for revegetation, and its availability is a persistent management issue for seed collectors and suppliers (Mortlock 2000b). Often, locally sourced seed is of limited supply resulting in harvest activities being relatively inefficient and costly. Both the amount of seed available for harvest and the quality of that seed will depend on stand health, seasonal variation in rainfall and temperature, masting, predation, and natural seed viability.

Conclusion

Current strategies for collecting native seed of south-west Western Australian flora for use in revegetation tend to follow a precautionary principle that advocates collecting seed from geographically restricted areas located close to revegetation sites. Ideally, appropriate seed collection areas should be defined according to species-specific local adaptation to site conditions. Because of the paucity of information on local adaptation from genetic and field studies, recommendations for appropriate seed collection areas are not available for most species utilised for restoration and revegetation in this region. However, the likelihood of local adaptation and hence the requirement to utilise more locally collected seed in revegetation programs, may be inferred from patterns of genetic differentiation among populations. In the absence of genetic data probable patterns of genetic differentiation may in turn be inferred by assessment of species-specific traits such as geographic distribution, pollen and seed dispersal, breeding system, life history traits (successional stage, annual, short-lived or long-lived perennial) and life form (herbaceous, shrub or tree).

We have suggested here a strategy for determining appropriate seed collection areas for south-west Western Australian flora commonly used for revegetation. We recommend taking into consideration a number of factors including the aim of the revegetation program, the characteristics of the revegetation site, species specific local adaptation, partitioning of genetic variation, and the availability and quality of local seed sources (Table 1). In many cases, a seed collection strategy where seed is sourced from a number of large healthy populations located a greater distance from the site to be rehabilitated but habitat matched for regional edaphic, climatic and environmental variables at the revegetation site may be appropriate. Such a strategy aims to prevent the introduction of highly maladapted genotypes whilst maximising genetic diversity and the potential for adaptation at the revegetation site in both the short and long term. Such an approach is especially advocated for small revegetation sites where the degree of environmental disturbance is significant or future changes to the environment are likely, where there are few local populations with which introduced material may interbreed and when local adaptation is not present. Seed collection areas may also be broadened for species where information suggests local adaptation and outbreeding depression is unlikely and significant partitioning of genetic variation due to restricted gene flow is not expected. In situations where local seed sources are not available or are of poor quality, seed collection areas will also have to be broadened and collections from a number of healthy populations matched from ecogeographic variables are recommended.

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Ant dispersal and predation affects the availability of seeds for old-field recolonisation in Western Australia

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Abstract

Seed arrival onto abandoned farmlands (old-fields) in south-western Australia can be limited by their proximity to native remnant vegetation. As the major seed-harvesting guild, ants could affect seed availability on old-fields by either: (1) affecting the dispersal of elaiosome-bearing seeds from adjacent remnants; (2) thieving the elaiosome from seeds without affecting their dispersal onto old-fields; or (3) predating seeds, which reduces the availability of seeds for dispersal. The relative importance of these ant-seed interactions will depend on the rates of ant-mediated seed dispersal from the remnants onto the old-field, as well as the rates of seed predation across these habitats. We sampled the ant communities within two old-fields, within the adjacent eucalypt woodland remnants and at the boundaries of these two habitats, using pitfall traps to determine the relative proportions of seed dispersers, elaiosome thieves and seed harvesters within each zone–ants were assigned to these groups on the basis of our observations of ant-seed interactions. During these observations, we followed the fate of elaiosome-bearing *Acacia* seeds that were offered to ants within each zone, primarily to estimate rates of seed dispersal and elaiosome thieving. We also offered eucalypt seeds to ants in feeding stations to estimate seed predation within each zone. We found that the relative proportions of seed dispersers, elaiosome thieves and seed harvesters were similar across zones, despite differences in the species composition between sites and a reduction in species richness in the old-fields. None of the *Acacia* seeds that we offered were dispersed from either remnant into the adjacent old-field. The majority of dispersal events were less than 3.6 m from the seed source (61%; $n = 74$) and dispersal beyond 20 m was rare (4%; maximum 28.1 m). Rates of elaiosome thieving and seed predation were not elevated in the old-fields compared with their rates in the other zones. Overall, the data indicate that ant-mediated seed dispersal onto old-fields was rare and seed predation by ants was similar across habitats.

Keywords: elaiosome, myrmechory, *Acacia acuminata*, *Eucalyptus loxophleba* subsp. *loxophleba*, old-field succession

Introduction

Seed availability onto abandoned farmlands (old-fields) in south-western Australia is limited–soil seed storage is uncommon and seed dispersal onto old-fields is generally limited by the distance to the seed source (Standish *et al.* 2007). However, the latter observation has not been confirmed for species whose seeds are dispersed by ants. Ants could potentially affect the dispersal of legumes and other native plants with elaiosome-bearing seeds adapted for this purpose (Davidson & Morton 1984; Beattie 1985). Indeed, myrmechory is a common dispersal mode among the flora of south-western Australia (Berg 1975; Milewski & Bond, 1982). Conversely, ants could remove the elaiosome without dispersing the seed ('aril robbing'; Andersen & Morrison 1998). We term this 'elaiosome thieving' to be consistent with the well-established terminology used to describe floral larceny (Inouye 1980). Ants can also predate seeds, usually without affecting their dispersal (Parsons 1968; Bell *et al.* 1993; Yates *et al.* 1995 but see Retana *et al.* 2004); we term these species 'seed harvesters' after Briese & Macauley (1977). So, ant-seed interactions can have both positive and negative outcomes (Berg 1975; Beattie 1985; Andersen 1988) which have implications for the availability of seeds on old-fields. The net outcome will depend on the movement of seed-dispersing ants between the native woodlands and the adjacent old-field, as well as the rates of seed predation across these habitats.

For many invertebrate taxa, the boundaries between habitats are broad transition zones rather than sharply defined edges (Dangerfield *et al.* 2003). Therefore, the movement of ants across boundaries is likely, and will be determined by the foraging distances and the competitive interactions between the species present in each habitat (Haering & Fox 1987; Adler & Gordon 2003; Ness 2004). The species present in old-fields are likely to include those that can survive the disturbances induced by clearing and cultivation, and will probably include seed dispersers such as *Melophorus* and *Rhytidoponera* and seed harvesters, such as *Pheidole* and *Monomorium* (Majer *et al.* 1987; Lobry de Bruyn 1990 cited in Hobbs *et al.* 1993).

The aim of our study was to determine the effect of ants on the availability of seeds within two old-fields in south-western Australia. We sampled the ant communities within two old-fields, their adjacent remnants and across the boundaries of these habitats to determine the relative proportions of seed dispersers, elaiosome thieves and seed harvesters. We assigned ant species to these groups on the basis of our observations during studies of ant-seed interactions. In these studies, we estimated rates of ant-mediated seed dispersal, elaiosome thieving and seed predation using feeding stations placed within the same zones. We considered the implications of our data for the recolonisation of old-fields by native woodland species.

Methods

Study sites

The study sites were two old-fields and their adjacent eucalypt woodland remnants ~4 km apart in the central wheat and sheep farming region of Western Australia. The climate of the region is extra-dry Mediterranean (Beard 1990). Native plant recolonisation of both old-fields is limited; the dispersal of wind-dispersed species decreases with distance from the adjacent woodland remnants (Standish *et al.* 2007). The woodland remnants included species of *Acacia, Gastrolobium, Lepidosperma, Daviesia, Goodenia* and *Velleia* (Standish *et al.* 2007), all of which might possess myrmechorous seeds (Berg 1975).

The Letchford Road old-field (7.3 ha; 31°18'S, 117°43'E) is bordered by Letchford Road along one length, a road reserve along another side, and by woodland on the other two sides. It is dominated by vegetative cover of non-native annual grasses (*Avena* spp., *Pentaschistis airoides*) and native grasses (*Aristida holathera, Austrostipa eremophila*). The adjacent remnant is a York gum (*E. loxophleba*)–wandoo (*Eucalyptus capillosa*)–mallee (probably *E. subangusta*) woodland; it is ~100 ha in size. The old-field at Pullen Road (22.3 ha; 31°20'S, 117°44'E) is bordered by Pullen Road, woodland and, on opposite sides, two cultivated paddocks. It is dominated by vegetative cover of non-native annual grasses (*Avena* spp.) with scattered *Acacia acuminata*. The adjacent remnant is York gum–wandoo–salmon gum (*E. salmonophloia*) woodland; it is ~100 ha in size. Both remnants that we studied are unusually large and intact compared with other remnants in the region (Yates & Hobbs 1997). Further details of the land-use histories of these sites are provided in Standish *et al.* (2006).

Five transects were set out at each site, 65 to 80 m apart and perpendicular to the boundaries of the old-field and remnant. The boundaries were separated by a dirt track ~2 m wide that ran between the woodland remnant and old-field at each site. Four zones along each transect were used throughout this study: 50 m into the remnant (50R) and 50 m into the old-field (50OF) and at the boundaries of the two habitats (*i.e.* 0 m into each habitat; 0R and 0OF). A map of this layout is provided in Standish *et al.* (2007).

Ant assemblages

Pitfall traps were used to sample the surface-active ant community at each site; five replicate pitfall traps (*i.e.* one per transect) were placed at each of the four zones. Pitfall traps consisted of a 44 mm diameter (150 mL) specimen vial inserted into the ground after removing a plug of soil with a purpose-built auger. Traps were flush with the ground and two-thirds filled with a 70:30 95%-ethanol:glycol mix. Traps were collected after 7 days and the samples were stored in 70% ethanol. Ants were identified to morphospecies and, where possible, to species, using the reference collection of Western Australian ants held at Curtin University of Technology. Samples are housed at Curtin University of Technology.

Ant-mediated seed dispersal

The observational unit was a 6 x 6 grid of filter paper discs (50 mm diameter) spaced 2 m apart, similar to that of Andersen (1988a). At each site, two replicate grids were placed at each of the four zones; grids were placed at transects 1 and 5 so as to minimise repeated sampling of ants from the same nests. The grids at 0R and 0OF were approximately 3 m apart. One *Acacia acuminata* seed was placed on each disc. We chose *A. acuminata* (hereafter *Acacia*) because it is common at the study sites and its seeds are readily available. The seeds were collected by Greening Australia (Northam) prior to May 2004 and weighed ~16 mg each; they were not fresh but this did not seem to diminish their attractiveness to ants. We did not expect, nor observe, seed rain from the *Acacia* trees within the study area as this usually occurs soon after pod development and seed set in December (R J Standish, pers. obs.).

Sampling was conducted between 13 and 20 March 2005 and was stratified so that one replicate was conducted in the morning (started between 7.25 and 7.55 hrs) and one in the evening (started between 14.25 and 15.45 hrs). The maximum daily temperatures for this period recorded at the nearest (Kellerberrin) climate station ranged from 26.2–38.5 °C (Bureau of Meterology 2005). Initiation of the evening sample was deliberately delayed on the hottest days until ant foraging was observed. After three hours the fate of seeds was recorded as either: dispersed (seed not within 3 cm of the disc); elaiosome thieved (seed minus elaiosome within 3 cm of the disc); or unmoved (seed with elaiosome within 3 cm of the disc).

When an ant was seen collecting a seed during the observation period, the ant was followed until it reached its nest or abandoned the seed. If the ant took the seed into its nest, then dispersal was inferred; the dispersal distance was measured, and an ant was sampled for later identification. Also, ants seen feeding on the elaiosome but not dispersing the seed (*i.e.* eliasome thieves) were sampled for later identification. If a seed was removed but the ant not seen, that seed was recorded as dispersed and an additional seed added to the disc to allow further observations. We assumed these seeds were dispersed by ants rather than by other seed-dispersing fauna (*i.e.* birds or rodents) because these animals were relatively inactive during our observations.

Seed predation by ants

At each site, five replicate feeding stations (one per transect) were placed at each of the four zones. A feeding station consisted of a 5 cm plastic petri dish and lid glued to a 10 cm x 10 cm plywood board; there were three 5 mm entrances spaced equidistant around the perimeter of the dish (Yates *et al.* 1995). Each feeding station contained 10 *Eucalyptus loxophleba* subsp. *loxophleba* (York gum) seeds. The York gum seeds are small (*i.e.* < 1 mm in diameter) and have no elaiosome. Eucalypt seeds are generally eaten by ants (Yates *et al.* 1994a; Yates *et al.* 1995; Ruthrof *et al.* 2002). In addition, non-feeding stations were placed at each of the four zones on transects one and five to estimate the removal of seeds by the wind. The non-feeding stations had Tac-gel (Formula 3, Rentokil Initial Pty Ltd, NSW, Australia) applied to plywood board to prevent ants from entering the feeding station. Feeding and non-feeding stations were placed out on 12 March 2005 and left in place for 24 hrs when the seeds remaining were counted. Stations that had seeds missing upon collection were restocked and left in place for a further 24 to 48 hours, during which time they were frequently checked to establish if seeds were removed by ants, and to sample these ants for identification.

Statistical analysis

Detrended correspondence analysis (DCA; Hill & Gauch 1980) was used to explore differences in ant assemblages among zones. DCA arranges groups along ordination axes, based on the composition of taxa, and does not force association among groups. Relative to other ordination techniques, DCA has improved performance when data are heterogeneous (Hill & Gauch 1980). Abundance data was transformed to log (x + 1) before ordination, which reduced the impact of very abundant species on the result. The program PC-ORD (McCune & Mefford 1999) was used for these analyses.

We used a two-factor ANOVA to compare the abundance of seed dispersers, eliasosome thieves, and seed harvesters in the pitfall traps; and to compare the species richness of the ants sampled using pitfall traps. The factors were zone (fixed) and site (fixed). We used the same test to compare the numbers of *Acacia* seeds that were dispersed, had their elaiosomes thieved or were unmoved from the discs. Data were log transformed where necessary to meet the assumptions of ANOVA. Analyses were done using SPSS (SPSS Inc. 2002).

Results

Ant assemblages

Ant assemblages were separated primarily by site along axis 1 of the ordination (Fig. 1). Within each site, ant assemblages within the remnant (zones 50R and 0R) were distinct from those within the old-field (zones 50OF and 0OF) along axis 2, and these differences more distinct at Pullen (Fig. 1). However, these differences were primarily due to those ants not associated with seeds (Table 1). Of the 22 taxa associated with seeds in the studies of ant-seed interactions and sampled in at

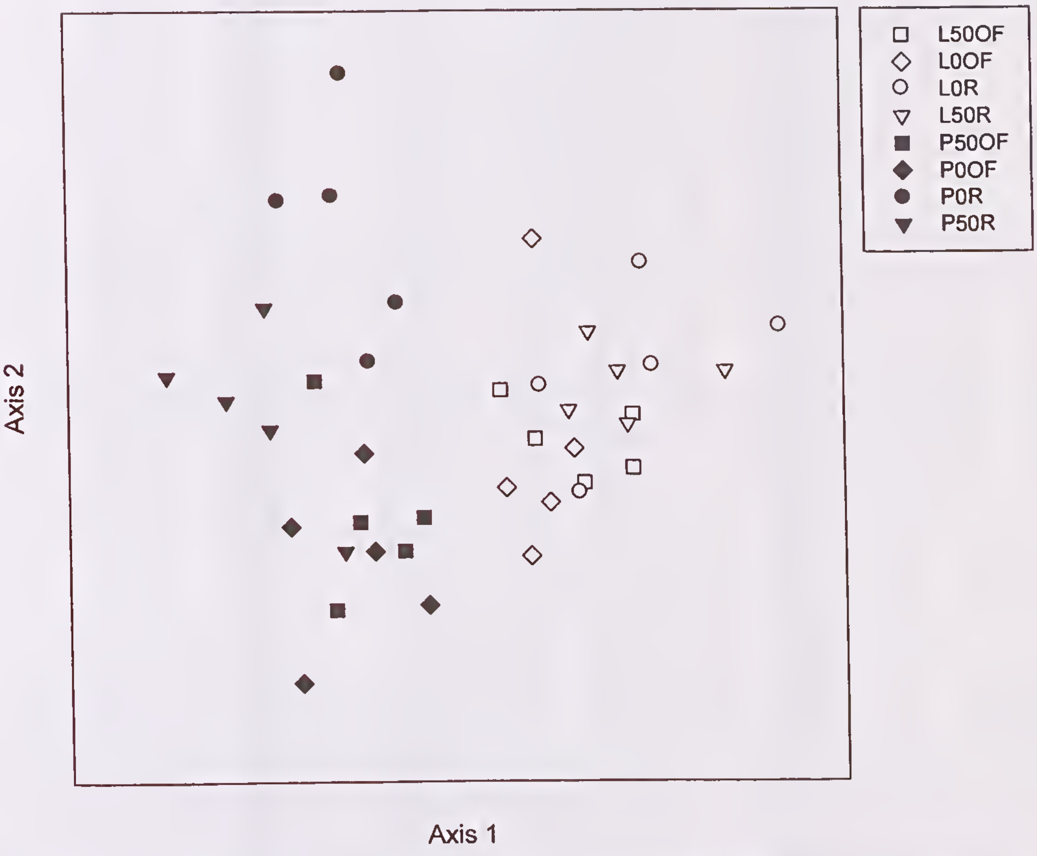

Figure 1. Ordination of ant assemblages at Letchford (open symbols) and Pullen (filled symbols) located within zones. Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field. R^2 axis-1 = 0.28; R^2 axis-2 = 0.13.

Table 1

Summary of ant assemblages sampled using pitfall traps at Letchford and Pullen. The ants associated with seed dispersal, elaiosome thieving and seed predation in the studies of ant-seed interactions are shaded grey and labelled 'Y' = commonly associated; '1' = observed on a single occasion. The other ants that were not observed interacting with seeds (*i.e.* not associated with seeds) are unshaded. Data are mean ± SE.

Taxon	Letchford 50OF	OOF	0R	50R	Pullen 50OF	0OF	0R	50R	Seed disperser	Elaiosome thief	Seed harvester
Dolichoderinae											
Iridomyrmex bicknelli	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Iridomyrmex chasei	103 ± 79	573 ± 211	656 ± 263	959 ± 266	0 ± 0	0 ± 0	0.4 ± 0.4	0 ± 0		Y	
Iridomyrmex chasei concolor	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3.6 ± 2.4	24.4 ± 9.1	59 ± 58	8.8 ± 7.5		Y	
Iridomyrmex dromus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.8 ± 1.8			
Iridomyrmex hartmeyeri gp. sp. JDM849	0 ± 0	0 ± 0	0.4 ± 0.4	0.4 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Iridomyrmex mattiroloi splendens	0 ± 0	1.6 ± 1.3	0 ± 0	0.2 ± 0.2	4.4 ± 4.1	0.2 ± 0.2	1 ± 1	4.8 ± 4.8			
Iridomyrmex rufoniger suchieri POP1	0.2 ± 0.2	0.6 ± 0.6	1 ± 0.6	1.2 ± 0.9	0.2 ± 0.2	4.4 ± 3.9	0 ± 0	9.6 ± 9.6			
Iridomyrmex viridiaenens	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	1 ± 1	0.6 ± 0.4	2.4 ± 2.2	Y		
Irodomyrmex bicknelli brunneus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0.6 ± 0.4	0.2 ± 0.2			
Tapinoma sp.	2 ± 2	0.8 ± 0.8	0.6 ± 0.6	1.8 ± 1.2	0.2 ± 0.2	2.2 ± 0.8	0.4 ± 0.2	0.6 ± 0.6			
Formicinae											
Camponotus capito ebeninithorax	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0.2 ± 0.2			
Camponotus cinereus amperei	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Camponotus cowlei	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Camponotus nigriceps	0 ± 0	0 ± 0	0.2 ± 0.2	0.4 ± 0.4	0 ± 0	0 ± 0	0.4 ± 0.4	0.6 ± 0.2			
Camponotus claripies	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2			
Camponotus oetkeri	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Camponotus gibinotus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0			
Melophorus bruneus complex sp. JDM791	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0 ± 0	1 ± 1	0 ± 0	1.2 ± 0.4	Y		
Melophorus bruneus gp JDM 600	0 ± 0	0 ± 0	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1		
Melophorus insularus	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.6 ± 0.4			
Melophorus JDM176	0.8 ± 0.8	2.4 ± 2.4	2.8 ± 1.7	6 ± 3.8	0 ± 0	2.6 ± 1.2	0 ± 0	26.4 ± 13.5			
Melophorus JDM472	0.4 ± 0.4	3.4 ± 3.1	0.4 ± 0.4	0 ± 0	3 ± 3	1.6 ± 1.1	3.2 ± 3.2	4 ± 3.7			
Melophorus JDM787	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Melophorus ludius sulla	0 ± 0	1.8 ± 1.8	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	7.6 ± 4.3			
Melophorus mjobergi	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Melophorus potteri	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.4	0 ± 0	0.4 ± 0.2			
Melophorus sp. near *aeneovirens* (JDM545)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	2 ± 1			
Melophorus sp.	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Melophorus turneri	1.2 ± 0.8	0.2 ± 0.2	1.4 ± 1.1	1 ± 0.7	6.2 ± 5.9	0 ± 0	0 ± 0	7.8 ± 3	Y		
Melophorus turneri perthensis	0 ± 0	2.6 ± 2.6	0.8 ± 0.5	0.8 ± 0.8	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	Y		
Melophorus wheeleri	7 ± 2	6.4 ± 4.5	1 ± 1	5.6 ± 5.6	8.8 ± 5.3	7.2 ± 4.1	0 ± 0	0 ± 0	Y	1	

Stigmacros ?JDM1015	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Stigmacros JDM341	0 ± 0	0 ± 0	0.6 ± 0.4	0.4 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Ponerinae											
Anochetus armstrongi	0 ± 0	0.4 ± 0.4	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0			
Odontomachus ruficeps	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.6 ± 1.3	=		
Ectatomminae											
Rhytidoponera metallica	0.4 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.2	5.2 ± 1.4	0.8 ± 0.3	Y	1	
Rhytidoponera violacea	2.2 ± 0.5	4 ± 1.9	3.6 ± 1.6	0.8 ± 0.3	1.2 ± 0.8	0.8 ± 0.3	1.4 ± 0.6	4.8 ± 1.8	Y		
Myrmicinae											
Crematogaster frivola	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.8 ± 0.8		1	
Crematogaster JDM428	0 ± 0	0 ± 0	0.4 ± 0.4	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1		
Epopostruma lattini	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Meranoplus diamidiatus	0 ± 0	0 ± 0	0 ± 0	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Meranoplus diversus	0 ± 0	0.2 ± 0.2	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Meranoplus JDM423	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		1	
Monomorium aithoderum	3.2 ± 3.2	0 ± 0	0 ± 0	1.8 ± 1.1	0 ± 0	0 ± 0	0.8 ± 0.8	29 ± 24		Y	Y
Monomorium anthracinum	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium bicorne	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium centrale	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.4 ± 0.9	0 ± 0	0.2 ± 0.2	0 ± 0		1	
Monomorium fieldi	0.6 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		1	
Monomorium laeve	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.8 ± 0.8	0.2 ± 0.2	3.2 ± 2.7			
Monomorium rothsteini	20 ± 12	24 ± 11	3 ± 2.7	8.4 ± 6	119 ± 80	116 ± 39	1 ± 0.7	0 ± 0		Y	
Monomorium rufonigrum	0 ± 0	0 ± 0	0 ± 0	0.8 ± 0.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium silaceum	2.4 ± 1.6	1.2 ± 0.7	2.4 ± 1.1	0.4 ± 0.2	0 ± 0	1 ± 1	0 ± 0	0 ± 0			
Monomorium sordidum	2.6 ± 2.6	1.8 ± 1.8	2.2 ± 1.3	0.8 ± 0.8	21 ± 7	23 ± 10	48 ± 38	34 ± 10		Y	
Monomorium stictonotum	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0			
Monomorium sydneyense	1 ± 1	0 ± 0	0.2 ± 0.2	4 ± 3.5	0 ± 0	0 ± 0	0 ± 0	2.2 ± 1.9			
Pheidole ampla	0.2 ± 0.2	0 ± 0	0 ± 0	0.4 ± 0.4	4 ± 3.5	0 ± 0	1 ± 1	0.2 ± 0.2			Y
Pheidole ampla perthensis	0.4 ± 0.4	1 ± 0.7	0.8 ± 0.5	0 ± 0	4.6 ± 4.6	0.6 ± 0.6	0 ± 0	2.4 ± 1.7	1		
Pheidole hartmeyeri	1.6 ± 1.3	0 ± 0	0.2 ± 0.2	0 ± 0	15 ± 14	15 ± 12	0.2 ± 0.2	0 ± 0	1		
Pheidole JDM164	0 ± 0	1.2 ± 1.2	1.8 ± 1.3	0.6 ± 0.4	0.8 ± 0.8	0 ± 0	0 ± 0	9.4 ± 7.1			
Pheidole JDM177	2 ± 2	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0.2 ± 0.2	2 ± 2	1		
Solenopsis clarki	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2			
Tetramorium impressum	0.4 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1	1	Y
Tetramorium striolatum	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0 ± 0			
Tetramorium viehmeyeri	1.2 ± 1.2	1.4 ± 0.9	0 ± 0	0 ± 0	0 ± 0	0.8 ± 0.5	0 ± 0	0 ± 0			

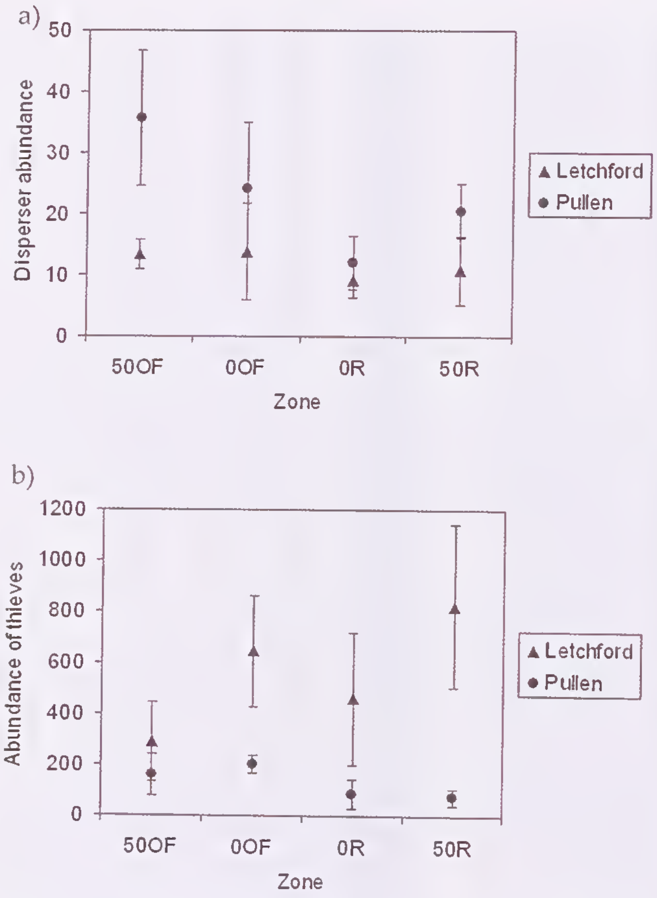

Figure 2. Mean abundance (± SE) of a) *Acacia*-seed dispersers and; b) elaiosome thieves sampled using pitfall traps (n = 5). Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field.

least two pitfall traps, 21 were sampled on both sides of the boundary and one, *Tetramorium impressua*, was only sampled in the Letchford old-field (Table 1). Also, this species was recorded dispersing an *Acacia* seed 93 cm within the Pullen old-field. Two taxa (*Meranoplus* JDM423 and *Crematogaster* JDM428) were recorded during the studies of ant-seed interactions and not sampled in the pitfall traps.

Acacia seed dispersers were more abundant at Pullen than at Letchford and tended to be more abundant in the old-field than in the woodland at Pullen (Fig. 2a; MS (site) = 0.88; d.f. = 1,32; P = 0.01; MS (zone) = 0.31; d.f. = 3,32; P = 0.08; MS (site x zone) = 0.12; d.f. = 3,32; P = 0.43). Thieves were more abundant at Letchford than at Pullen, and at Letchford the 50R zone had much higher abundance of thieves than the 50OF zone (Fig. 2b). This is principally due to the high abundance of *Iridomymex chasei* in the woodland compared to its abundance in the old-field at Letchford (Table 1). At Pullen, the abundance of thieves was similar across zones (Fig. 2b; MS (site) = 3.60; d.f. = 1,32; P < 0.001; MS (zone) = 0.47 ; d.f. = 3,32; P = 0.1; MS (site ′ zone) = 0.66; d.f. = 3,32; P = 0.04). The abundance of the three (confirmed) York gum seed harvesters was too low and variable to establish a pattern.

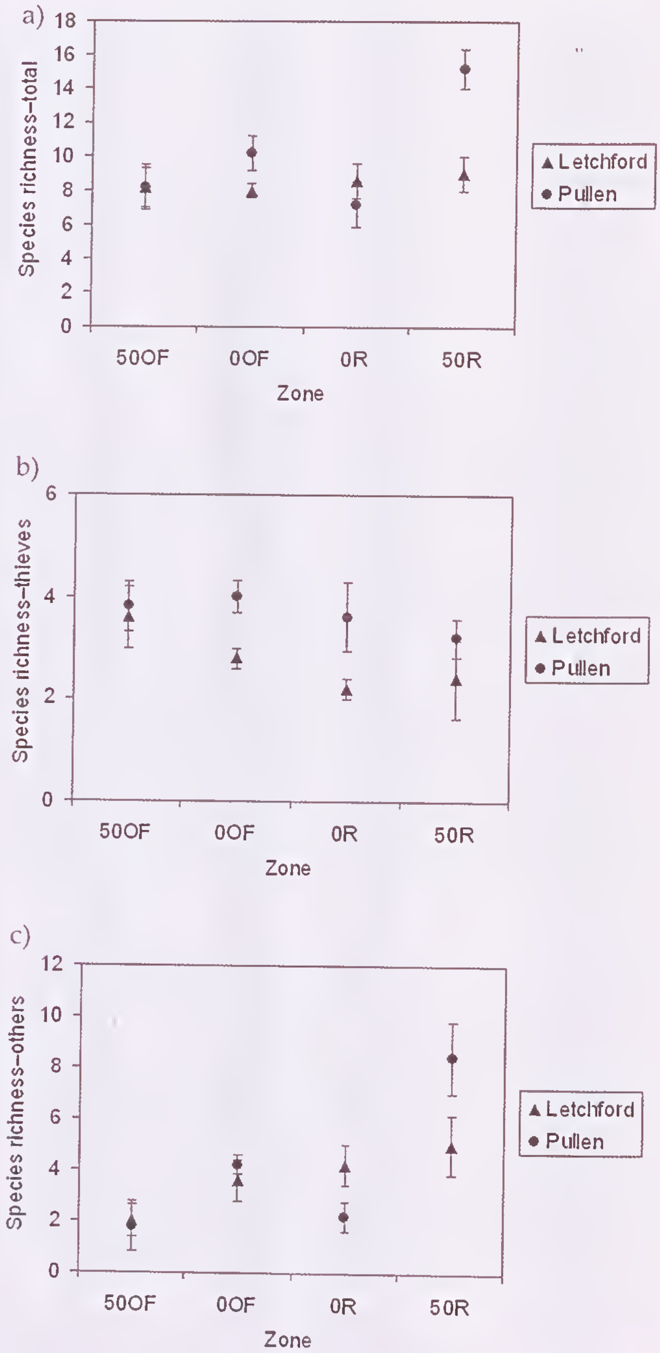

Figure 3. Comparison of species richness of ants sampled using pitfall traps: a) all ants b) elaiosome thieves and c) other ants not associated with seeds. Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field. Values are means ± SE; n = 5.

The species richness of ants was similar between sites and zones except for the 50R zone at Pullen, which had a much higher species richness (Fig. 3a; MS (site) = 30.63; d.f. = 1, 32; P = 0.03; MS (zone) = 36.83; d.f. = 3,32; P = 0.002; MS (site x zone) = 27.49; d.f. = 3,32; P = 0.009). The species richness of seed dispersers and seed harvesters was similar between sites and zones (data not shown). The species richness of thieves was higher at Pullen (Fig. 3b; MS (site) = 8.1; d.f. = 1, 32; P= 0.015) and the species richness of others (those not recorded on seeds) was highest in the 50R zone (Fig. 3c; MS (zone) = 0.378; d.f. = 3, 32; P < 0.001). The ant which was numerically dominant differed between the two sites; *I. chasei concolor* was abundant at Letchford and *I. chasei* was abundant at

Pullen. Functionally, these two species are likely to be similar.

Ant-mediated seed dispersal

Of the 576 *Acacia* seeds offered, 76.7 % were dispersed, 11.6 % had their elaiosome removed *in situ* while the remainder (11.7 %) were unmoved at the end of the observation period. A total of 74 dispersal events were observed, of which 70 resulted in the seed entering a nest. Some ant colonies were responsible for more than one dispersal event. Thirteen species were recorded dispersing seeds (Table 1), but most dispersal events were by various species of *Melophorus* (28 observations) *Rhytidoponera violacea* (22), or *Iridomyrmex viridiaeneus* (10). Foragers of *Melophorus* were only active when it was too hot for the other species.

Most (78%) dispersal events were < 6 m (mean 4.83 ± 0.66 m), but foragers of *R. violacea*, *I. viridiaeneus*, *Melophorus bruneus* complex JDM791 and *Melophorus wheeleri* dispersed seeds over greater distances (Fig. 4a). Dispersal distances were similar within each habitat (Fig. 4b). There were no seeds dispersed from the remnants into the old-fields. However, seeds were taken from a site on the edge of the old-field over a distance of 28.1 m into the remnant by workers from a large *I. viridiaeneus* colony.

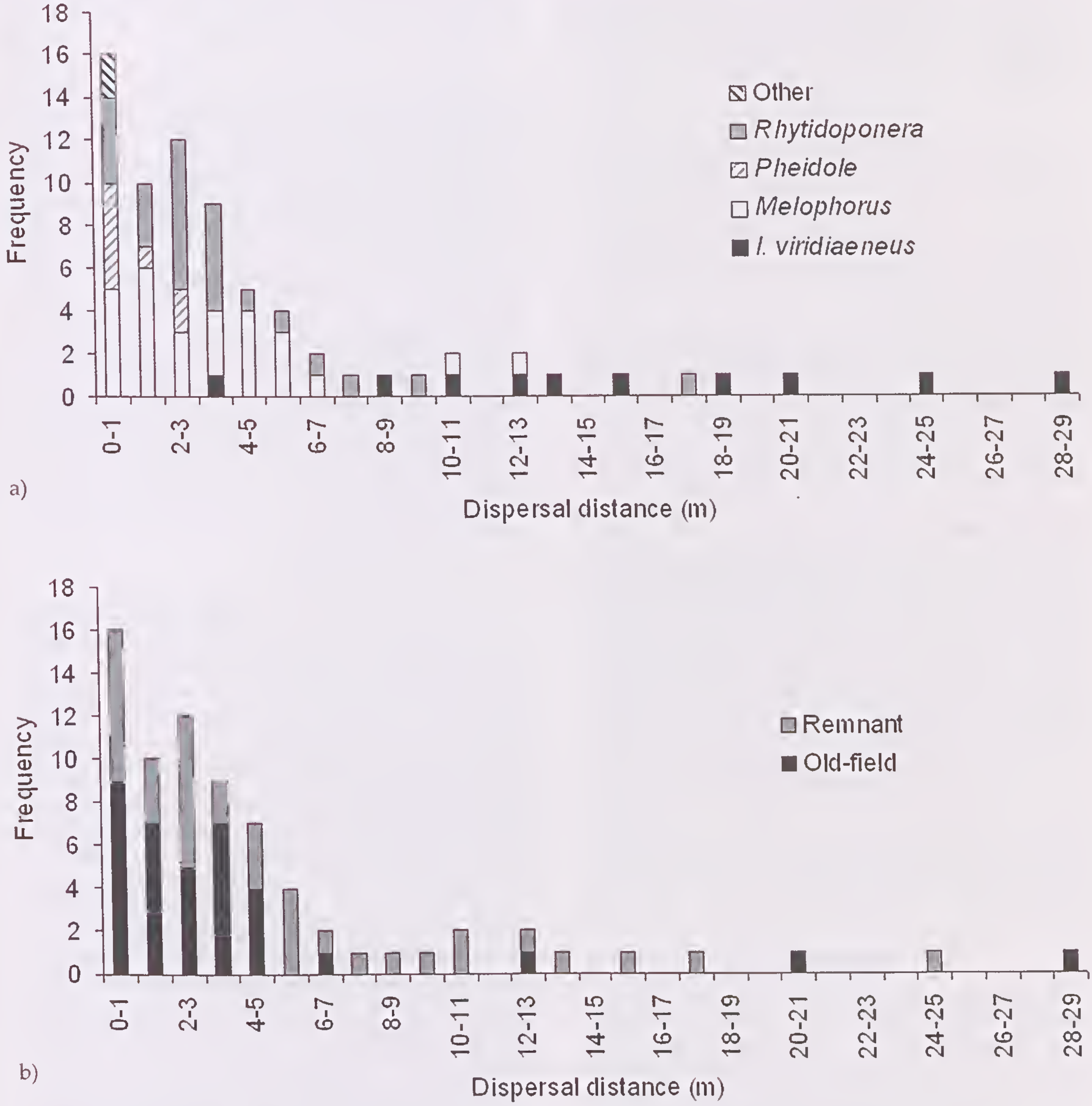

Figure 4. Dispersal distances (m) of *Acacia* seeds from filter paper discs according to: a) ant species and b) habitat.

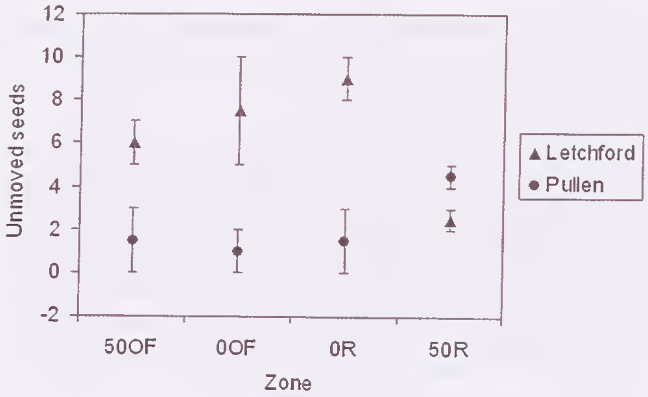

Figure 5. The mean number (± SE) of *Acacia* seeds, of 36 offered, that were unmoved at the end of the three hour periods of observation (n = 2). Zones: 50R = 50 m into the remnant, 0R = at the remnant edge, 0OF = at the old-field edge, 50OF = 50 m into old-field.

The *Acacia* seeds that had their elaiosome removed became unattractive to ants dispersing seeds. Twelve taxa were recorded thieving elaiosomes (Table 1). Of the 39 thieves collected, 20 (51%) were one or other of five species of *Monomorium* and 14 (36%) were the numerically abundant *Iridomyrmex* (*I. chasei* and *I. chasei concolour*). None of the *Monomorium* or *Iridomyrmex* species dispersed seeds.

There were more unmoved seeds at Letchford than at Pullen, except in the 50R zone where there were more unmoved seeds at Pullen (Fig. 5; MS (site) = 68.06; d.f. = 1,8; P = 0.002; MS (zone) = 2.40 ; d.f. = 3,8; P = 0.59; MS (site x zone) = 18.23; d.f. = 3,8; P = 0.03). The frequency of seed dispersal and eliaosome thieving was similar among zones and between sites (P> 0.05 for all).

Seed predation by ants

At Pullen, seeds had disappeared from 10 feeding stations (35 % of total seeds offered) from within all zones. The stations were restocked and seeds continued to disappear. Foragers of *Pheidole ampla* and *Monomorium aithoderum* were observed collecting seeds from two stations. Seeds were also missing from four non-feeding stations (12.5% of total). Also, *Pheidole ampla* and *Pheidole* JDM177 were observed removing seeds on dishes at Pullen prior to the study.

At Letchford, seeds had disappeared from one feeding station (1.5 % of total seeds offered). The station was restocked and there was no evidence that ants were feeding at the station as these seeds remained in the station. Seeds were also missing from two of the non-feeding stations (11.25% of total).

Discussion

We found that ant-mediated seed dispersal onto old-fields was rare: none of the *Acacia* seeds that we offered were dispersed from either remnant into the adjacent old-field. Instead, the majority of dispersal events were less than 3.6 m from the seed source. We found that the relative proportions of seed dispersers, elaiosome thieves and seed harvesters were similar across zones, despite differences in the species composition between sites and a reduction in species richness in the old-fields. Moreover, rates of elaiosome thieving and seed predation were not elevated in the old-fields compared with their rates in the other zones. Lastly, there were differences in ant assemblages and ant-seed interactions between sites despite their proximity.

Ant assemblages

The ant assemblages in the woodlands and the old-fields were different; however, the species that were observed interacting with seeds were present in both habitats. The species richness of ants unassociated with seeds was highest in the woodlands. Although these taxa were not associated with seeds in this study, it is likely that some of the omnivorous *Melophorus* species collect seeds (Briese & Macauley 1981).

The Pullen woodland had more leaf and twig litter compared with the Letchford woodland, which could explain the higher species richness at this site. Secondly, pitfall traps are likely to sample active foragers, whose activity will be modified by the ground cover surrounding the trap; trapping efficiency increases with increasing simplification of the ground cover (Majer 1980a). This may account for the very high abundance of *I. chasei* in the Letchford woodland. Surveying nest densities may give a more accurate picture of relative abundance between habitats, and would be an easy task for those species with large visible nests, such as *Melophorus wheeleri* complex (which includes *M. wheeleri*, *M. turneri* and *M. turneri perthensis*), *Rhytidoponera* spp. and *I. viridiaeneus*, all common seed dispersers in this study (Table 1). We recognise too, that we have probably missed sampling some ants that are active at other times of the year. Similarly, our observations of ant-seed interactions may or may not be typical of these interactions at other times of the year (*e.g.* December, when *Acacia* seeds fall).

Ant-mediated seed dispersal

We did not record any ant-mediated seed dispersal from the remnants into the adjacent old-fields. However, it is likely to occur occasionally, as the main seed-dispersing species are present in both habitats, their nests are near to the boundary and the maximum dispersal distances are sufficient to affect dispersal between habitats. In particular, *Rhytidoponera* is one of most important seed dispersers in Australia (Gove *et al.* 2007; Dunn *et al.* 2008). Also, they do not have specific habitat preferences (Bisevac & Majer 1999; May & Heterick 2000) which suggests that the boundary would not represent a barrier to dispersal by ants belonging to this genus.

Field-based studies of ant-mediated seed dispersal typically generate a dispersal curve similar to the one in this study, with most seeds dispersed short distances (*i.e.* < 1m; Gomez & Espadaler 1998). Dispersal distance has been shown to increase with worker body size (Gomez & Espadaler 1998, Ness *et al.* 2004), and this was the case in our study. *Iridomyrmex viridiaeneus* and *R. violacea*, the largest species recorded taking seed, were the only taxa to disperse seeds beyond 13 m. However, small *Melophorus* workers were a notable exception; they dragged seeds much larger than themselves over large distances to their nest (up to 12 m). The maximum dispersal distance recorded in the literature is 180 m (Whitney 2002), compared with 28.1 m recorded here. However, well-worn foraging trails of *I. viridiaeneus* extended from the colony well beyond the zone where seed dispersal was recorded in the old-field at Pullen, so it is likely that seed would have been taken greater distances by this species if seeds were placed at greater distances from their nests.

Generally, not all seeds that are carried reach a nest. In our study, four seeds were dropped *en route* to a nest. On one occasion, a *Melophorus* forager was disturbed by a predatory spider and abandoned the seed. In another case, an I. *viridiaeneus* forager dropped a seed on a well-formed *I. viridiaeneus* foraging trail, and the seed remained there, ignored by the stream of foragers that passed during the observation period. Such seeds can potentially be picked up by other ants and taken to their nests.

Typically, the elaiosome thieves are small ants that appear as though they would have difficulty dragging the seed to their nest. Elaiosome thieving usually occurs near to the seed source and prevents further dispersal by myrmechorous species. Where elaiosome thieving occurs away from the parent plant, it can increase the likelihood of seed germination (Pizo & Oliveira 2001; Passos & Oliveira 2002). In most cases, however, the seed will remain on the soil surface or it may be taken by a seed predator.

The old-field and woodland habitats were floristically and structurally distinct (Standish *et al.* 2007), yet *Acacia*-seed removal rates were similar as was the abundance of ant seed dispersers. This result contrasts with that of Grimbacher & Hughes (2002), who found seed removal rates of both native and exotic seeds were significantly lower in weedy sites than in undamaged bushland. In our study, removal rates across both habitats (76.7% within 3 hours) were high compared with rates reported in other studies (Majer 1980b and references cited). This suggests that seeds were in short supply.

Seed predation by ants

The percentage of York gum seeds removed from the feeding stations was low, whereas there was a higher than expected loss of seeds from the non-feeding stations. Yates *et al.* (1995) found 21% of seeds were removed from feeding stations within 24 hrs and only 0.25% of seeds were missing from non-feeding stations in the same period; they also found that seed removal was patchy–depending on whether or not ants recruited to the feeding stations. It is unclear why we had high rates of seed loss from the non-feeding stations. It is possible that the Tac-gel had lost its effectiveness as a barrier, allowing ants to enter and remove seeds.

Three species were observed predating seed at Pullen and none were observed at Letchford. However, the three species recorded predating seeds at Pullen were sampled at Letchford, but at lower relative abundance (mean = 2.0 ± 1.3 workers/pitfall at Letchford compared with 9.3 ± 6.2 at Pullen). The three seed harvesters were recorded in both the remnant and old-field habitats, but they were sampled too infrequently to compare their abundance between these habitats. It is likely that some of the other *Pheidole* and *Monomorium* taxa sampled in the pitfall traps at the two sites would also predate eucalypt and other seeds. The availability of eucalypt seeds in Pullen and Letchford old-fields is limited; instead the seed supply is dominated by native and exotic grasses such as *Avena barbata* (Standish *et al.* 2007). No doubt the seeds of these species are attractive to some ants, for example, the husks of *A. barbata* seeds were found discarded around the entrances to *Melophorus wheeleri* nests on these old-fields.

Ants feed on eucalypt seeds *in situ* (Wellington 1989) or store them in their nests (Andersen & Yen 1985; Wellington & Noble 1985; Hughes & Westoby 1992). Some of the stored seeds can geminate (Andersen & Yen 1985; Hughes 1991), although small seeds such as those of salmon gum are unlikely to germinate if they are buried more than a few centimetres below the soil surface (Yates *et al.* 1995; Grant *et al.* 1996). Eucalypt recruitment generally occurs after a large-scale disturbance event, such as fire, when ant harvesters are satiated and safe sites for germination are abundant (Wellington & Noble 1985; Andersen 1987; Yates *et al.* 1995). However, it is conceivable that predation could limit recruitment after fire on old-fields where the local seed supply is limited.

Implications for old-field recolonisation

Ant-mediated long-distance dispersal events are rare, so these are unlikely to be significant for returning native plants to old-fields (Cain *et al.* 2000; this study). The majority of ant-mediated seed dispersal events were less than 3.6 m from the seed source, so we might expect a gradual spread of ant-dispersed woodland species into the old-field as seen elsewhere (*e.g.* Bossuyt *et al.* 1999). On the other hand, it has recently been suggested that kangaroos and emus can act as non-standard dispersers of myrmechorous seeds, which means that long-distance dispersal events remain a possibility (Calviño-Cancela *et al.* 2008). However, in our case there was no evidence of the spread of woodland species into the old-fields. There are several possible reasons for this. First, recruitment can be limited by competition with exotic grasses (Standish *et al.* 2008). Moreover, recruitment is inherently rare because for most species it is contingent upon the unusual coincidence of large-scale disturbance events, such as wildfire, to trigger seed fall and germination, followed by summer rainfall to ensure seedling establishment (Yates *et al.* 1994b; Ruthrof *et al.* 2003; Yates *et al.* 2003; Standish *et al.* 2007). Taken together, the evidence suggests that we should expect the return of native woodland species to old-fields to be slow or non-existent.

For old-fields such as Pullen and Letchford, woodland species may not return without assistance. The removal of the exotic grasses followed by direct seeding will be necessary to ensure their restoration (Standish *et al.* 2007; Standish *et al.* 2008). There are no quantitative data on the success of grass removal and direct seeding for the restoration of old-fields, but the factors that effect the recruitment of broadcast seeds onto rehabilitated mine-sites are likely to be similar, and seed predation by ants is among these (Majer 1980b; Majer & Abbott 1989; Majer *et al.* 2007). In this context, ant predation is likely to play a more significant role in the availability of seeds for old-field recolonisation.

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Triodia caelestialis (*Triodieae*: Chloridoideae: Poaceae), a new species from the central Kimberley, Western Australia

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Abstract

Triodia caelestialis G. Armstrong, a new species from the central Kimberley of north-western Australia is described based upon morphological characters and reproductive traits. The taxon is distinguished from its sister species *T. acutispicula* Laza. by differences in inflorescence morphology and allocation of resources to sexual reproduction. *T. caelestialis* produces approximately five times more seed than *T. acutispicula* resulting in higher seedling densities and does not produce stolons whereas *T. acutispicula* allocates greater resources to asexual reproduction through the production of numerous stolons. A predicted species range map is produced using BIOCLIM modeling and the morphological effect of a leaf axil fungal infection is discussed.

Keywords: *Triodia*, Poaceae, Kimberley, BIOCLIM

Introduction

During the course of research into the reproductive strategies of *Triodia* species at Mornington Wildlife Sanctuary, in the central Kimberley, it became apparent that specimens identified as *T. acutispicula* Laza. may not have constituted a single taxon. All individuals in populations identified as *T. acutispicula* share the same unusual floret morphology, described here for the first time; however, some individuals are highly stoloniferous while others produce no stolons. Based on the premise that this difference in allocation of resources to reproduction indicated a taxonomic difference data were collected on the morphology and reproductive strategies of the two morphotypes to determine if a taxonomic reassessment was warranted.

Previous taxonomic work on *Triodia* by Mant *et al.* (2005), using molecular data, resolved a clade of 'soft' leaved species, those with a central row of stomata on the abaxial surface, to be nested within the 'hard' leaved species of *Triodia*. Though differing from previous infrageneric groupings based on floral and leaf anatomy (Lazarides 1997), this classification did not dispute previous species definitions based on the same data sets. It would not be unreasonable therefore, to assume taxa within the 'soft' clade sharing similar floral characteristics be assigned as sister species. The two morphotypes of interest in this research share 'soft' leaves and the same unusual floret morphology suggesting sister species status, thus allowing a direct comparison between them. Growing sympatrically suggests observed differences are due to genetic, not environmental factors and the use of both morphological and reproductive data provides a good basis for this taxonomic reassessment.

Methods

In determining the specific status of *T. caelestialis* morphological characters were considered along with comparative reproductive traits of its sister species *T. acutispicula*. Morphological descriptions and measurements are based on fresh samples collected at locations at Mornington Wildlife Sanctuary and 'Mt. House' Station. Reproductive data were collected on populations of both taxa at Mornington Wildlife Sanctuary. Specimens *of T. caelestialis* have also been observed in the King Leopold Ranges Conservation Park. Coordinates for these locations are in Table 1. The following *T. acutispicula* herbarium specimens were examined to identify possible specimens of *T. caelestialis* thereby identifying further localities for the latter, Perth 00486442, Perth 00486469, Perth 00879274, Perth 00486426, Perth 06960170, Perth 02384035, Perth 00486515 and AD96127037.

Table 1

Location names and coordinates (GDA 94) of specimens of *T. caelestialis* collected and observed.

Location	Coordinates	
Mornington Wildlife Sanctuary		
Research Centre	17°30.627'S	126°6.530'E
Boundary Pool	17°29.538'S	126°5.404'E
Sir John Gorge	17°31.181'S	126°12.791'E
Narrie Range	17°24.938'S	126°13.244'E
Mt. House	17°05.098'S	125°47.304'E
King Leopold Ranges Conservation Park	17°06.930'S	125°10.037'E

Reproductive traits were recorded from observation of flowering times and quantifying reproductive allocation to stolon and seed production and seed to floret ratios at the 'Research Centre' populations of *T. acutispicula* (17°30.489'S 126°6.317'E) and *T. caelestialis* (17°30.445'S 126°5.804'E). Within both of these populations five 5 x 5 m quadrats were placed semi-randomly at least 5 m apart. Quadrats were selected as the nearest patch of uniform *Triodia* located at a right angle to a 20 m transect at each 5 m interval. Distances from the transect ranged from 0 to 10 m due to either patches of bare ground or the presence of trees. Within each quadrat stolons were quantified by allocation to one of the following categories; 0–25, 26–50, 51–75, 76–100 and >100. Stolon number was estimated in categories due to the inability of distinguishing a true stoloniferous shoot, which forms an independent ramet, from a young side branch. The number of seedlings from the current season were also counted within each quadrat. Seedlings were identified by being less than 10 cm tall and lacking an established root base. These counts were conducted on 16th June 2008. Seed number and seed to floret ratio were determined by counting the number of reproductive culms in a 1 x 1m quadrat within the first quadrat, counting the number of spikelets on a subsample of 10 randomly selected culms, and counting the number of fertile florets and full caryopses of 70 spikelets. This quadrat was selected subjectively as representing an average culm density within the first 5 x 5 m quadrat. These counts were made in February 2008.

Seed and floret counts were non-normal and of unequal variance and were therefore compared using the paired samples Wilcoxon test in Programme R http://www.r-project.org/.

The predicted species range map was prepared using the Biomap function in BIOCLIM 5.1 (Houlder *et al.* 2008) http://cres.anu.edu/outputs/anuclim.html), and intersecting this with sandstone habitat. Input data for Biomap were location and height data of known samples and Geoscience Australia 9 Second DEM Version 2.1. The distribution of sandstone was determined from Australian 1:250,000 Geological Series maps.

Choosing the bioclimatic variables to include in the model was based on assumptions regarding the most biologically meaningful variables and experimentation to look at the outcomes of combinations of variables. Using too many or too few variables either over-fits or under-fits the model resulting in a predicted range across the entire north of the country or only encompassing the known localities. Many variables had little or no effect and it was found that using only 'Precipitation of wettest period' and 'Precipitation Seasonality' at full range produced a map that appears a realistic compromise between the possible extremes.

Taxonomy

Triodia caelestialis G. Armstrong, *sp. nov.*

Planta caespitosa, nec resinosa nec stolonifera, 40 cm alta x 60 cm lata. Foliorum laminae flexuosae et torsivae ad 30 cm x 2 mm. Culmi reproductivi 160 (> 200) cm alti x 4–5 mm lati. Inflorescentia panicula in maturitate aperta, 18–40 cm (plerunque 30 cm) longa, ramis primariis 11–26. Pedicelli spicularum lateralium 2–5 mm longarum compositi; spiculae terminalis pedicello ad 1.5 cm longo. Spiculae in quoque ramo usque 14 lineares, teres plerunque apice campanulato globum facientes. Flosculi 6–10, illis 1–3 basi fertibus, 0–2 caryopsibus in quoque spicula. Glumae 15–24 mm, linearo lanceolatae, glabrae, acuminatae, nervis 6–12. Lemma 5–7 mm longum, glabrum praeter seriebus paralellis pilorum adpressorum in quoque latere cristae angustae in dimidio indurato; lobi et aristae terni, lobis et aristis lateralibus 6–11, lobo et arista mediis 10–12 mm longis. Palea 0.6 cm longa. Callus 1–2 mm longus pilis lateralibus densis adpressis obtectus. Caryopsis 3 mm longa anguste oborata.

T: Mornington Wildlife Sanctuary Research Centre, central Kimberley, W.A. 17°30.627'S 126°6.530'E 21st January 2008 *G. Armstrong* holo: PERTH 07842791; iso: CANB, NT.

Caespitose, non-resinous, non-stoloniferous perennial forming compact, non-branching tussocks 40 cm tall x 60 cm wide. *Non-reproductive* culms to 4 cm long, found only within the basal leaf sheaths*, therefore not hummock forming. *Leaf blades* originating predominantly from within the basal sheaths; flexuose and spiraling, to 30 cm x 2 mm, slightly pungent; abaxial surface nerved in the median band and nerveless to margin, 'soft'; leaf orifice with hairs to 4 mm; ligule a membrane with cilia to 1mm total length, membrane 1/3 the length of the cilia. *Reproductive culms* smooth, 160–>200 cm tall x 4–5 mm wide, with 3–5 prominent nodes to 6 mm diameter, often red on, above and below the node for c. 5 mm. *Culm leaf sheath* smooth, less than ½ internode length differing from basal leaves by ligule membrane being ¼ the length of the cilia and leaves being very pungent. *Inflorescence* a panicle, contracted when immature, open at maturity, 18–40 (average 30) cm long with 11–26 primary branches with secondary branching of the basal branches; lower panicle branch 6–19 (average 10) cm long; rachis 0.5–1.5 mm diam.; branches and pedicels scabrous; simple hairs to 0.5 mm long sometimes on the sides of the branches at the axil; pulvinus commonly found on the inner side of the panicle branch at the axil forming a yellow crenulate surface, to 2 mm long, often growing beyond the outer edges of the branch. *Pedicels* of lateral spikelets of similar length, 2–5 mm long; terminal spikelet pedicel longer than laterals, to 15 mm long; hairs to 1 mm long sometimes present at pedicel axis. *Spikelets* up to 14 per branch; linear, terete, commonly with campanulate apex, forming a ball when dry. *Florets* 6–10, the basal 1–3 florets fertile with 0–2 caryopsis per spikelet, the apical 5–7 florets infertile, contiguous, consisting of only the lemma lobes, the middle 2 or 3 of these florets with wider lemma lobes than those below or above and having minimal distance between them on the rachilla flare at this point into a star shape; the lobes of these florets range from purple to straw-coloured, contrasting with the bright green nerves running up the centre of the lobe; uppermost florets reduced to awns (Fig. 2A). *Glumes* longer than spikelet without awns; +/- equal length, 15–24 mm, linear-lanceolate, scarious, glabrous, acuminate,

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* see note under fungal infection

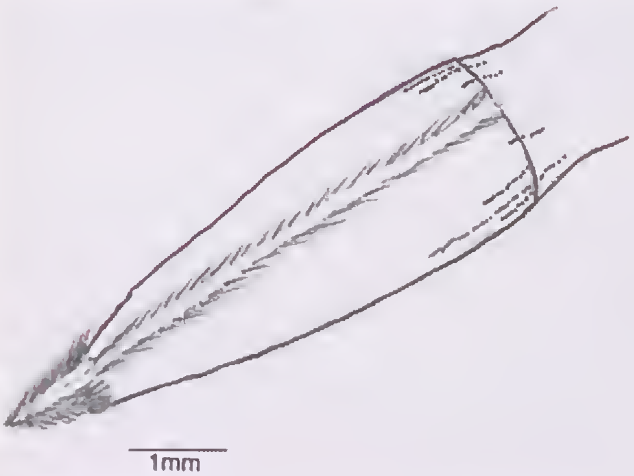

Figure 1. Lemma with 2 parallel rows of hairs running up the centre of the lower half. This contrasts with the glabrous lemma of *T. acutispicuta* Lazarides (1997) Fig. 10.

6–16 nerved in lower half, reduced to at least 3 in upper half, outer surface grading from smooth at base to asperulous above. *Lemmas* 5–7 mm long excluding lobes and callus, bitextured, indurate below, cartilaginous above with a hard thickening at the demarcation line on the inner surface 1–4 mm below sinus of lobes, often enclosing the edges of the palea, glabrous apart from two parallel rows of adpressed hairs either side of a narrow ridge, running up the centre of the lower indurate half (Fig. 1); lower indurate half of lemma often brown when mature which does not indicate the presence of a caryopsis; 3 lobes and awns with lateral awns shorter than mid-awn, mid-lobe and awn 10–12 mm long, lateral lobes and awns 6–11 mm; awns twisted and recurved, 3 nerved. Rachilla 3 mm long. *Palea* 6 mm long, bitextured, cartilagenous in the lower ¾, hyaline in the upper ¼, narrowly oblong, emarginate apex; keel margin ciliate, flaps hyaline. *Callus* 1–2 mm long, lateral dense adpressed hairs to 0.5 mm long, tip glabrous, sometimes curved, pungent. *Caryopsis* 3 mm long narrowly obovate, shallow groove lengthwise along inner side.

Distribution and Habitat. Specimens have been collected and observed in the central Kimberley region on Mornington Wildlife Sanctuary, 'Mt. House' Station and King Leopold Ranges Conservation Park. The herbarium specimens Perth 00486515 and Perth 02384035 have been identified as *T. caelestialis* extending the known range of *T. caelestialis* to "NE side of CRA camp, Ellendale, 24.3km from Gibb River Road 17°30'S 124°50'E" and "Charnely River Crossing, 55km Nth Beverley Springs 16°43'S 125°27'E" respectively. The coordinates given for Perth 02384035 refer to Beverley Springs Homestead and the actual site 55km north of this point would be located at approximately 16°13'S 125°27.4'E. Populations range from a few dozen individuals to several hectares, predominantly on quartzite sandstone pediment along the edge of a range or isolated outcrop, extending marginally onto the surrounding depositional sand (Fig. 2B). In the sandy areas stands of *T. caelestialis* and *T. acutispicula* abut and intermix at their margins. *T. epactia* stands abut those of *T. caelestialis* on the upward slope of sandstone ranges. A population grows on shale on Mt. House Station. This population abuts *T. aeria*.

Etymology. Alluding to the star shaped cluster of infertile florets at the apex of the spikelet; caelestialis: heavenly body, star.

Distinguishing characters. Current keys for identifying *Triodia* species are adequate to place *T. caelestialis* in *T. acutispicula* with some minor adjustments. In Lazarides (1997) the character of "plants resinous" at 4A must be ignored while accepting "blade on the lower (abaxial) surface strongly nerved or grooved in a median band". This is corrected in Lazarides *et al.* (2005). Sharp and Simon (2002) also places *T. caelestialis* successfully in *T. acutispicula* providing one of the final characters "culms to 1.5m tall" is treated as conservative.

T. caelestialis is distinguished from its closest relative *T. acutispicula* by the absence of stolons and exposed non-reproductive culms. Taller mean (160 cm vs. 140 cm) and maximum (>200 cm vs. 170 cm) reproductive culms in *T. caelestialis* and greater number of panicle branches (26 vs. 13) and spikelets per branch (14 vs. 7). The lemma of *T. caelestialis* has 2 parallel rows of hairs on the back of the lemma while the lemma of *T. acutispicula* is glabrous. The hairs at the leaf orifice are longer in *T. caelestialis* (4 mm vs. 1.5 mm) and the ligule is longer in total length (1 vs. 0.5 mm) and proportionally different with the membrane 1/3 the length of the cilia vs. equal length.

Phenology. Specimens of *T. caelestialis* at all localities within Mornington Wildlife Sanctuary flowered over a period of approximately 6 weeks from late January to the middle of March 2008. Specimens observed at 'Mt. House' Station and King Leopold Ranges National Park in late March 2008 retained reproductive culms but had lost all florets suggesting a similar flowering period. Specimens at the type locality were burnt in October 2006, regrew and flowered during January to March 2007.

Results of Reproductive Trait Analysis. The average number of seeds per floret is significantly greater in *T. acutispicula* at 0.8 than *T. caelestialis* at 0.53 (V = 503, p= 0.004), there is no significant difference between the number of fertile florets per spikelet, 2.5 to 2.4 (V = 234, p= 0.07) but there is significantly more spikelets per culm, 106 to 27.9 (V= 0, p-value = 0.005) and culms per m^2, 184 to 87.4 (V = 1, p= 0.003) in *T. caelestialis* than *T. acutispicula*. This results in a much greater number of seeds per m^2 in *T. caelestialis*, 10,337 compared with 1,950 in *T. acutispicula*. The ratio of seeds to florets is similar at 1:4.7 and 1:3 for *T. caelestialis* and *T. acutispicula* respectively. The mean number and standard deviation of seedlings in 5 x 5 m plots at approx. 4 months age for *T. caelestialis* was 28 (SD=25) compared with a mean of 0.2 (SD=0.45) for *T. acutispicula*. No stolons were recorded in *T. caelestialis* plots while *T. acutispicula* plots contained a mean of 85 (SD=20).

The lack of stolons in *T. caelestialis* reflects resource partitioning into a direct reproductive trait, however, the taxon shows limited vegetative reproduction through the separation of parts after senescence of the centre of the plant (Fig. 2D).

Predicted range. The range predicted for *T. caelestialis* from the BIOCLIM model shows a continuous band from

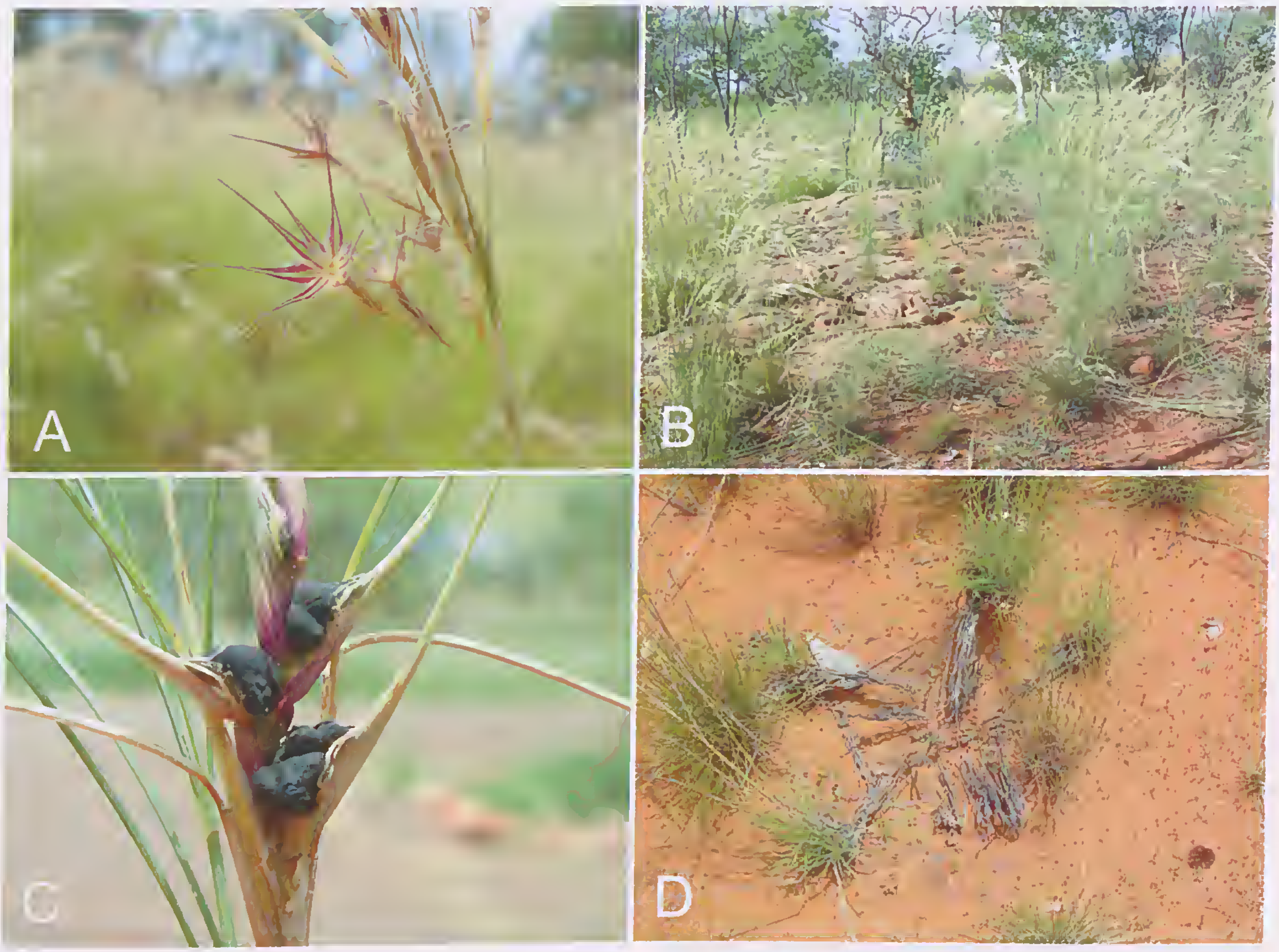

Figure 2. Photographs of *T. caelestialis*. A – florets showing star structure; B – habit and usual habitat; C – fungal infection in leaf axils; D – division of adult plant.

the Dampier Peninsula following the King Leopold Ranges across to Mornington in the east. Two outlying populations are predicted, one south of Wyndam and the other further east into the Victoria River district in the Northern Territory. No specimens of either *T. caelestialis* or *T. acutispicula* have been collected from the Northern Territory to support this prediction. The disjunction between the western and eastern Kimberley populations is also treated as an artifact due to the small sample size in the model and it is assumed these populations are joined. Removing the Dampier Peninsula due to lack of suitable sandstone habitat gives a predicted range following the King Leopold Ranges in a curve around the bottom of the Kimberley. (Fig. 3). The error in the model must be acknowledged and it is deemed biologically reasonable to assume the actual range may extend north into areas of higher precipitation.

Fungal infection. Individuals of both *T. acutispicula* and *T. caelestialis* show fungal infection in leaf axils, identified as the ergot *Claviceps* sp. in *T. acutispicula* PERTH 00879274. However, a diagram of the Ascostromata *Nigrocornus scleroticus* on *T. epactia* in Ryley (2003) has the same appearance as those found on *T. acutispicula* and *T. caelestialis*. When this fungal infection occurs on *T. caelestialis* the non-reproductive culms elongate and appear externally as in *T. acutispicula*. Clay (1988) hypothsised that the close association of fungal hyphae with rapidly dividing plant cells would enhance the ability of the fungus to gain nutrient from the host plant while influencing plant growth through the release of phytohormones. This may explain the unusual elongation of non-reproductive culms in infected *T. caelestialis* (Fig. 2C).

Discussion

Morphological data alone distinguishes *T. caelestialis* from other *Triodia* species including its sister species *T. acutispicula*. However, this data only provides a pattern from which to derive a taxonomic delimitation which has no need of either a species definition or speciation process (Harrison 1998). The use of ecological data, in this case reproductive traits, allows the utilisation of information regarding the processes which are acting and have acted to unify a group of individuals and distinguish them from others. The reproductive traits, acting as multiple covarying characters, are a usable unified taxonomic character. The extent to which resources are devoted to sexual or asexual reproduction through seed density, floret number and stolon presence

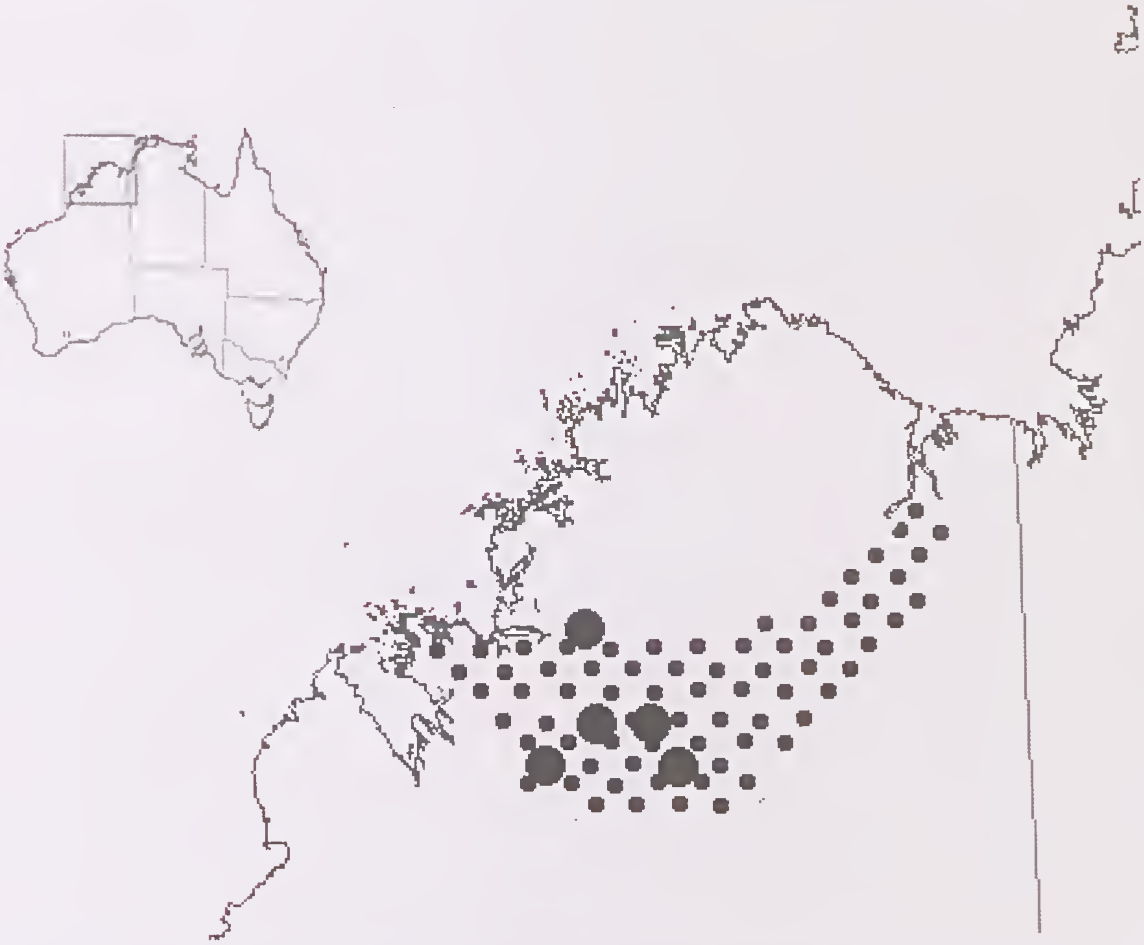

Figure 3. Predicted distribution range shown with small dots and known localities shown with large dots.

differs between the two related taxa and are taken to be the consequences of divergent evolution. Growing sympatrically reaffirms the genetic basis for this conclusion. The delimitation is therefore, given extra rigour through the use of the ecological data which reveals evolutionary processess. This conclusion provides a useful position from which to begin studies of speciation in *Triodia*.

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